Status and Trends in Demography of Northern Spotted Owls, 1985–2003

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ABSTRACT

We analyzed demographic data from northern spotted owls (*Strix occidentalis caurina*) from 14 study areas in Washington, Oregon, and California for 1985–2003. The purpose of our analyses was to provide an assessment of the status and trends of northern spotted owl populations throughout most of their geographic range. The 14 study areas made up approximately 12% of the range of the subspecies and included federal, tribal, private, and mixed federal and private lands. The study areas also included all the major forest types that the subspecies inhabits. The analyses followed rigorous protocols that were developed a priori and were the result of extensive discussions and consensus among the authors. Our primary objectives were to estimate fecundity, apparent survival (ϕ), and annual rate of population change (λ) and to determine if there were any temporal trends in these population parameters. In addition to analyses of data from individual study areas, we conducted 2 meta-analyses on each demographic parameter. One meta-analysis was conducted on all 14 areas, and the other was restricted to the 8 areas that constituted the Effectiveness Monitoring Plan for northern spotted owls under the Northwest Forest Plan. The average number of years of reproductive data per study area was 14 (range = 5–19), and the average number of recapture occasions per study area was 13 (range = 4–18). Only 1 study area had <12 years of data. Our results were based on 32,054 captures and resightings of 11,432 banded individuals for estimation of survival and 10,902 instances in which we documented the number of young produced by territorial females.

The number of young fledged (NYF) per territorial female was analyzed by testing a suite of a priori models that included (1) effects of age, (2) linear or quadratic time trends, (3) presence of barred owls (*Strix varia*) in spotted owl territories, and (4) an even-odd year effect. The NYF varied among years on most study areas with a biennial cycle of high reproduction in even-numbered years and low reproduction in odd-numbered years. These cyclic fluctuations did not occur on all study areas, and the even–odd year effect waned during the last 5 years of the study. Fecundity was highest for adults ($\bar{x} = 0.372$, SE = 0.029), lower for 2-year-olds ($\bar{x} = 0.208$, SE = 0.032), and very low for 1-year-olds ($\bar{x} = 0.074$, SE = 0.029). Fecundity was stable over time for 6 areas (Rainier, Olympic, Warm Springs, H. J. Andrews, Klamath, and Marin), declining for 6 areas (Wenatchee, Cle Elum, Oregon Coast Range, Southern Oregon Cascades, Northwest California, and Simpson), and slightly increasing for 2 areas (Tyee, Hoopa). We found little association between NYF and the proportion of northern spotted owl territories where barred owls were detected, although results were suggestive of a negative effect of barred owls on the Wenatchee and Olympic study areas. The meta-analysis on fecundity indicated substantial annual variability with no increasing or decreasing trends. Fecundity was highest in the mixed-conifer region of eastern Washington ($\bar{x} = 0.560$, SE = 0.041) and lowest in the Douglas-fir (*Pseudotsuga menziesii*) region of the Oregon coast ($\bar{x} = 0.306$, SE = 0.039).

We used Cormack–Jolly–Seber open population models and Program MARK to estimate apparent survival rates of owls >1 year old. We found no differences in apparent survival rates between sexes except for 1 area (Marin), which had only 6 years of data. Estimates of apparent survival from individual study areas indicated that there were differences among age classes with adults generally having higher survival than 1- and 2-year-olds. Apparent survival rates ranged from 0.750 (SE = 0.026) to 0.886 (SE = 0.010) for adults, 0.626 (SE = 0.073) to 0.886 (SE = 0.010) for 2-year-olds, and 0.415 (SE = 0.111) to 0.860 (SE = 0.017) for 1-year-olds. These estimates were comparable to survival rates from previous studies on the subspecies. We found evidence for negative time trends in survival rates on 5 study areas (Wenatchee, Cle Elum, Rainier, Olympic, and Northwest California) and no trends in survival on the remaining areas. There was evidence for negative effects of barred owls on apparent survival on 3 study areas (Wenatchee, Cle Elum, and Olympic). Survival rates of adult owls on the 8 Monitoring Areas generally were high, ranging from 0.85 (SE = 0.009) to 0.89 (SE = 0.010), but were declining on the Cle Elum, Olympic, and Northwestern California study areas. The meta-analysis of apparent survival indicated differences among regions and changes over time with a downward trend in the mixed-conifer and Douglas-fir regions of Washington. The meta-analysis of apparent survival also indicated that there was a negative association between fecundity and survival the following year, suggesting a cost of reproduction on survival. This effect was limited to the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir region of the Oregon Cascade Mountains.

We used the reparameterized Jolly–Seber method (λ_{RJS}) to estimate annual rate of population change of territorial owls in the study areas. This estimate answers the question, Are these territorial owls being replaced in this geographically open population? Point estimates of λ_{RJS} were <1.0 for 12 of 13 study areas. The analyses provided strong evidence that populations on the Wenatchee, Cle Elum, Rainier, Olympic, Warm Springs, H. J. Andrews, Oregon Coast Ranges, and Simpson study areas were declining during the study. The mean $\hat{\lambda}_{RJS}$ for the 13 study areas was 0.963 (SE = 0.009), suggesting that populations over all the areas were declining about 3.7% per year during the study. The mean $\hat{\lambda}_{RJS}$ for the 8 monitoring areas for the Northwest Forest Plan was 0.976 (SE = 0.007) compared to a mean of 0.942 (SE = 0.016) for the other study areas, a 2.4-versus-5.8% decline per year. This suggested that owl populations on federal lands had higher demographic rates than elsewhere; thus, the Northwest Forest Plan appeared to have a positive effect on demography of northern spotted owls. Populations were doing poorest in Washington, where apparent survival rates and populations were declining on all 4 study areas. Our estimates of λ_{RJS} were generally lower than those reported in a previous analysis ($\hat{\lambda}_{RJS} = 0.997$, SE = 0.003) for many of the same areas at an earlier date. The possible causes of population declines include but are not limited to habitat loss from timber harvest and fires, competition with barred owls, and weather patterns.

KEY WORDS

Estodo y Tendencias en la Demografia del *Strix occidentalis caurina*, 1985–2003

RESUMEN

Analizamos datos demográficos de búhos moteados norteños (*Strix occidentalis caurina*) de catorce áreas de estudio en los estados de Washington, Oregón y California durante el periodo 1985–2003. El propósito de nuestro análisis fue generar una evaluación del estado y de las tendencias de las poblaciones de búhos a través de la mayor parte de su extensión geográfica. Las catorce áreas de estudio comprendían aproximadamente el doce por ciento de la extensión de esta subespecie y comprendían tierras federales, tribales, privadas y una mezcla de tierras federales y privadas. Las áreas de estudio también incluían los principales tipos de bosques que habita la subespecie. Los análisis seguían protocolos rigurosos que fueron desarrollados a priori y fueron el resultado de discusiones prolongadas y el consenso de los autores. Nuestros objetivos principales eran: estimar la fecundidad, supervivencia aparente (ϕ) y tasa anual de cambio de población (λ) para determinar si había algunas tendencias temporales dentro de estos parámetros de población. Además de los análisis de los datos de las áreas de estudio individuales, realizamos dos meta-análisis en cada parámetro demográfico. Un meta-análisis se realizó en las catorce áreas y el otro se restringió a las ocho áreas que constituían el Effectiveness Monitoring Plan (Plan Monitor de Eficacia) para *Strix occidentalis caurina* bajo el Northwest Forest Plan (Plan Forestal del Noroeste). El promedio de número de años de datos de reproducción por área de estudio era catorce (rango $= 5–19$), y el promedio de número de ocasiones de recaptura por área de estudio era 13 (rango $= 4–18$). Sólo un área de estudio tenía <12 años de datos. Nuestros resultados se basaron en 32.054 capturas y revistas de los 11.432 individuos anillados para la estimación de supervivencia, y 10.902 ocasiones en que documentamos el número de crías producidas por hembras territoriales.

El número de pájaros volantones (NPV $=$ número de volantones que había abandonado el nido) por hembra territorial se analizó comprobando un grupo de modelos a priori que incluían: (1) los efectos de la edad, (2) tendencias cronológicas lineales o cuadráticas, (3) la presencia de *Strix varia* en territorios de *Strix occidentalis caurina*, (4) el efecto año par/impar. Estas fluctuaciones cíclicas no ocurrieron en todas las áreas de estudio, y el efecto año par/impar disminuía durante los últimos cinco años del estudio. La fecundidad era más alta para adultos (media $= 0.372$, error standar [ES] $= 0.029$), más baja para individuos de dos años (media $= 0.208$, ES $= 0.032$), y muy baja para individuos de un año (media $= 0.074$, ES $= 0.029$). Es más, encontramos que la fecundidad era estable durante el periodo del estudio en 6 áreas de estudio (Rainier, Olympic, Warm Springs, H. J. Andres, Klamath y Marin), posiblemente declinante para 6 áreas (Wenatchee, Cle Elum, Oregon Coast Range, Southern Oregon Cascades, Northwest California y Simpson), y ligeramente incremente para dos áreas. Encontramos poca relación entre NPV y la proporción de territorios de *Strix occidentalis caurina* donde se detectaba la presencia de *Strix varia*, si bien los resultados sugieren un efecto negativo de *Strix varia* en las áreas de Wenatchee y Olympic. El meta-análisis de fecundidad indicó bastante variabilidad anual sin ninguna tendencia creciente ni decreciente. La fecundidad era más alta en la región de coníferas mixtas de Washington oriental (media $= 0.560$, ES $= 0.041$) y más baja en la región de abeto Douglas (*Pseudotsuga menziesii*) en la región de Oregón litoral (media $= 0.306$, ES $= 0.039$).

Usamos modelos de población Cormack–Jolly–Seber y el Program MARK para estimar tasas de supervivencia aparente de búhos de >1 año. No encontramos ninguna diferencia en tasas de supervivencia aparente entre sexos, excepto para un área de estudio (Marin), que sólo tenía seis años de datos. Las estimaciones de supervivencia aparente de las áreas de estudios individuales indican que había diferencias entre grupos de edad y, en general, los adultos tenían una tasa de supervivencia más alta que los búhos de un y dos años. Las tasas de supervivencia aparente para búhos adultos varían de 0.750 (ES $= 0.026$) a 0.886 (ES $= 0.010$) y concordaban con las estimaciones de estudios previos acerca de la subespecie. Las tasas de supervivencia aparente para búhos de dos años varían de 0.626 (ES $= 0.073$) a 0.866 (ES $= 0.010$), y las de búhos de un año varían de 0.415 (ES $= 0.111$) a 0.860 (ES $= 0.017$). Encontramos muestras de tendencias cronológicas negativas en las tasas de supervivencia en cinco áreas de estudio (Wenatchee, Cle Elum, Rainier, Olympic y Northwest California) y ninguna tendencia en supervivencia en las demás áreas. Había muestras de efectos negativos de *Strix varia* en la supervivencia aparente en tres áreas de estudio (Wenatchee, Cle Elum y Olympic). Las tasas de supervivencia de búhos en las ocho Monitoring Areas (Areas de Control) eran generalmente altas, variando de 0.85 (ES $= 0.009$) a 0.89 (ES $= 0.010$); pero eran decrecientes en las áreas de estudio Cle Elum, Olympic y Northwest California. El meta-análisis de supervivencia aparente indica diferencias entre regiones y cambios con el paso del tiempo con una tendencia declinante en las regiones de coníferas mixtas y de abeto Douglas (Pseudotsuga menziesii) en Washington. El meta-análisis de supervivencia aparente también indica que había una asociación negativa entre la fecundidad y la supervivencia para el año siguiente, lo que sugiere que la reproducción tenía un efecto perjudicial en la supervivencia al año siguiente. Este efecto se limitó a las regiones de Washington y la región de abeto Douglas (*Pseudotsuga meniesii*) en las Montañas Cascadas de Oregón.

Usamos el método Jolly–Seber modificado (λ_{RJS}) que determina el estado de la población de búhos territoriales en las áreas de estudio. Contesta la pregunta, ¿Estos búhos territoriales están siendo reemplazados en esta población geográfica abierta? Estimaciones de puntos (λ_{RJS}) eran de <1.0 de doce de los trece áreas de estudio. Los análisis dieron indicios fuertes que las poblaciones en las áreas de estudio en Wenatchee, Cle Elum, Rainier, Olympic, Warm Springs, H. J. Andrews, Oregon Coast Ranges y Simpson disminuían durante el estudio. La media λ_{RJS} para las trece áreas de estudio era 0.963 (ES $= 0.009$), lo que sugiere que las poblaciones en todas las otras áreas de estudio disminuían aproximadamente en un 3,7% por año durante el estudio. La media λ_{RJS} para las ocho áreas de control del Plan Forestal del Noroeste era 0.976 (ES $= 0.009$) comparada con una media de 0.942 (ES $= 0.016$) para las otras áreas de estudio, una disminución de 2,4 versus 5,8% por año. Esto sugiere que las poblaciones de búhos en las tierras federales tenían tasas demográficas más altas que en otras áreas; por tanto, el Plan Forestal del Noroeste parece haber tenido un efecto positivo en la demografía de *Strix occidentalis caurina*. Las poblaciones que no prosperaban se encontraban en Washington, donde las tasas de supervivencia aparente y las poblaciones disminuían en todas (4) las áreas de estudio. Nuestras estimaciones de λ_{RJS} eran generalmente más bajas que las indicadas en un análisis previo ($\lambda_{RJS} = 0.997$, ES $= 0.003$) para muchas de las mismas áreas en fechas anteriores. Las causas posibles de estas disminuciones en población incluyen, pero no se limitan a: pérdida de hábitat debido a talas forestales e incendios forestales, competencia con *Strix varia* y ciclos climatológicos.

Le Statut et les Tendances dans la Démographie des Chouettes Tachetées Septentrionales, 1985–2003

RÉSUMÉ

Nous avons analysé des données démographiques des chouettes tachetées septentrionales (*Strix occidentalis caurina*) de 14 secteurs d'étude dans Washington, Oregon, et Californie pour la période de 1985–2003. Le but de notre analyse était de fournir une évaluation du statut et les tendances de la population des chouettes tachetées septentrionales à travers la plupart de leur gamme géographique. Les 14 secteurs d'étude ont compris approximativement 12% d'une variété de sous-espèces en incluant les terres fédérales, tribales, privées et un mélange de terres fédérales et privées. Les secteurs d'étude ont inclus aussi tous les types de forêts majeurs où les sous-espèces habitent. Les analyses ont suivi des protocoles rigoureux qui ont été développés a priori et étaient le résultat de discussions extensives et d'accords parmi les auteurs. Notre objectif primaire était d'estimer la fécondité, la survie apparente (ϕ), et le taux annuel de changement de population (λ) et déterminer s'il y avait des tendances temporelles dans ces paramètres de population. En assemblant les analyses de données des secteurs d'étude individuels, nous avons dirigé 2 méta analyses sur chaque paramètre démographique. Une méta analyse a été dirigée sur tous les 14 secteurs et l'autre a été limitée aux 8 secteurs qui ont constitué le plan de contrôle d'efficacité pour les chouettes tachetées septentrionales sous le Projet de Forêt Nord-ouest. Le nombre moyen d'années de données reproductives par les secteurs d'étude était de 14 (variation = 5–19), et le nombre moyen des occasions de recapture par le secteur d'étude était de 13 (variation = 4–18). Seulement 1 secteur d'étude avait moins de 12 années de données. Nos résultats ont été basés sur 32,054 captures et des portées de vue de 11,432 individus bandés pour l'estimation de survie, et 10,902 cas pour lesquels nous avons documenté le nombre de jeunes produits par les femelles territoriales.

Le nombre de petit d'hiboux (NYF) par femelle territoriale a été analysé en essayant des modèles a priori qui ont inclus: (1) les effets de l'âge, (2) les tendances de temps linéaires ou quadratiques, (3) les effets de chouettes striées (*Strix varia*), et (4) un effet d'année pair-impair. NYF a varié parmi les années pour la plupart des secteurs d'étude avec un cycle biennal de haute reproduction des années numérotées paires et de basse reproduction des années numérotées impaires. Ces variations cycliques n'ont pas eu d'effet sur tous les secteurs d'étude, et l'effet de l'année pair-impair a diminué pendant les 5 dernières années de l'étude. La fécondité était plus élevée pour les adultes (moyenne = 0,372, standard error [SE] = 0,029), moins élevée pour ceux âgés de 2 ans (moyenne = 0,208, SE = 0,032), et très basse pour ceux âgés d'un an (les moyennes = 0,074, SE = 0,029). De plus, nous avons trouvé que cette fécondité était stable progressivement pour 6 secteurs d'étude (Rainier, Olympic, Warm Springs, H. J. Andrews, Klamath, et Marin), en déclin probablement pour 6 secteurs (Wenatchee, Cle Elum, les chaînes de la côte d'Oregon, les chaînes méridionales d'Oregon, le Nord-ouest de la Californie, et Simpson), et en légère augmentation 2 secteurs (Tyee, Hoopa). Nous avons trouvé peu d'association entre NYF et la proportion de territoires des chouettes tachetées où les chouettes striées ont été détectées, bien que les résultats étaient suggestifs d'un effet négatif des chouettes striées pour le Wenatchee et les secteurs d'étude de l'Olympic. La méta analyse sur la fécondité a indiqué la variabilité annuelle substantielle sur les tendances avec ou sans croissance. La fécondité était plus élevée dans la région mixte de conifère de l'est de Washington (moyenne = 0,560, SE = 0,041) et moins élevée dans la région des Sapins de Douglas (*Pseudotsuga menziesii*) de la Côte d'Oregon (moyenne = 0,306, SE = 0,039).

Nous avons utilisé les modèles ⟨⟨Cormack–Jolly–Seber open population⟩⟩ et le Programme MARK et la statistique d'information théorique pour estimer les taux de survie apparents des chouettes âgés d'un an et plus. Nous n'avons pas trouvé de différences dans les taux de survie apparents entre les sexes à l'exception d'un secteur d'étude (Marin) qui avait seulement 6 années de données. Les estimations de survie apparente des secteurs d'étude individuels ont indiqué qu'il y avait des différences parmi les classes d'âge avec les adultes généralement ayant la plus haute survie que ceux âgés de 1 et 2 ans. Les évaluations de survie apparentes pour les vielles chouettes adultes variaient de 0,750 (SE = 0,026) à 0,886 (SE = 0,010) et étaient comparable aux estimations des études précédentes de la sous-espèce. Les taux apparents de survie de ceux âgés 2 ans variaient de 0,626 (SE = 0,073) à 0,886 (SE = 0,010), et ceux âgés de 1 an variaient de 0,415 (SE = 0,111) à 0,860 (SE = 0,017). Nous avons trouvé une évidence de tendance de temps négatif en taux de survie sur 5 secteurs d'étude (Wenatchee, Cle Elum, Rainier, Olympic et Nord-ouest de la Californie) et aucunes tendances de survie pour les secteurs restants. Il y avait des preuves d'effets négatifs sur le taux apparent de survie des chouettes striées dans 3 secteurs d'étude (Wenatchee, Cle Elum et Olympic). Les taux de survie des chouettes sur les 8 Secteurs de Surveillance étaient généralement élevés, s'étendant de 0,85 à 0,89; mais étaient en déclin sur les secteurs d'étude de Cle Elum, Olympic et le Nord-ouest de la Californie/La méta analyse de survie apparente a indiqué qu'il y avait des différences parmi les régions et des changements progressifs avec une tendance décroissante dans les régions mixtes de conifère et des Sapins de Douglas de l'état de Washington. La méta analyse de survie apparente a indiqué aussi qu'il y avait une association négative entre la fécondité et la survie pour l'année suivante. Cet effet a été limité aux régions des Sapin de Douglas, aux regions mixtes de conifère de Washington et de la région de Sapin de Douglas dans les chaînes de montagnes d'Oregon.

Nous avons utilisé une méthode modifiée de Jolly–Seber (λ_{RJS}) qui détermine le statut de la population des chouettes territoriales dans les secteurs d'étude. Cela répond à la question, ces chouettes territoriales sont-elles remplacées géographiquement dans cette ouverture de la population? Les points d'estimations de λ_{RJS} étaient <1.0 pour 12 des 13 secteurs d'étude. Les analyses ont fournie une forte preuve que les populations sur les secteurs d'étude de Wenatchee, Cle Elum, Rainier, Olympic, Warm Springs, H. J. Andrews, les chaînes la Côte d'Oregon et Simpson étaient en déclin pendant l'étude. La moyenne de λ_{RJS} pour les 13 secteurs d'étude était 0,963 (SE = 0,009), suggérant que les populations de chouettes de tous les secteurs déclinaient d'environ 3,7% par année pendant l'étude. La moyenne de λ_{RJS} pour les 8 secteurs de surveillance sur les terres fédérales était 0,976 (SE = 0,007) comparé à une moyenne de 0,942 pour les autres secteurs d'étude, environ 2,4 contre 5,8% de déclin par an. Ceci a suggéré que ces populations de chouettes sur les terres fédérales avaient de meilleurs taux démographique qu'ailleurs. A Washington, les populations de chouettes étaient les plus pauvres en nombre et le taux de survie apparent des populations était en déclin sur tous les 4 secteurs d'étude. Nos estimations de λ_{RJS} étaient généralement plus basses que celles reportées dans une analyse précédente (λ_{RJS} = 0,997, SE = 0,003) pour la plupart de ces mêmes régions à une date précédente. Les causes possibles de ces déclins de population inclues, mais pas exclusivement, à la perte d'habitat dû au déboisement et aux feux de brousse, la compétition avec les chouettes striées et les conditions climatiques. Ainsi le Projet Forestier Nord-ouest de Forêt s'est avéré d'avoir un effet positif sur la démographie de chouettes tachetées septentrionales.

Contents

INTRODUCTION

The northern spotted owl is a medium-sized, nocturnal owl that inhabits coniferous forests along the Pacific Coast of North America from southern British Columbia to central California (Gutiérrez et al. 1995). Adult spotted owls are territorial, exhibit high nest-site fidelity, and occupy relatively large home ranges (Forsman et al. 1984, Carey et al. 1990, Thomas et al. 1990). In contrast, juvenile spotted owls are highly mobile and typically do not acquire territories until they are 1–3 years old (Franklin 1992, LaHaye et al. 2001, Forsman et al. 2002). Northern spotted owls feed primarily on small mammals, especially northern flying squirrels (*Glaucomys sabrinus*) in Washington and Oregon and woodrats (*Neotoma* spp.) in southwestern Oregon and California (Barrows 1980; Forsman et al. 1984, 2001; Ward et al. 1998). The subspecies is closely associated with old forests throughout most of its range (Forsman et al. 1984, Thomas et al. 1990) but is common in young redwood (*Sequoia sempervirens*) forests in northwestern California (Diller and Thome 1999) and occurs at low densities in young Douglas-fir forests of the northern Oregon Coast Range (Glenn et al. 2004).

Because of the association between northern spotted owls and old forests, conservation of the owl and its habitat has been extremely contentious among environmentalists, the timber industry, land managers, and scientists since the early 1970s (Forsman and Meslow 1986, Thomas et al. 1990, Durbin 1996, Gutiérrez et al. 1996, Marcot and Thomas 1997, Noon and Franklin 2002). This controversy started when it became apparent that federal agencies were harvesting old forests at levels that were not sustainable (Parry et al. 1983). In spite of these concerns, the

U.S. Congress continued to increase harvest levels of old forests on federal lands during the 1970s and 1980s, until harvest levels on federal lands in western Oregon and Washington reached a peak of nearly 2.7 billion cubic feet per year in the late 1980s (Parry et al. 1983, Haynes 2003). As the rate of harvest increased, field surveys suggested that loss of old forests was leading to a decline in number of northern spotted owls (Forsman et al. 1984, Anderson and Burnham 1992). Meanwhile, management options decreased, litigation increased, and a number of committees, task forces, and work groups were organized to develop solutions that were biologically sound and politically acceptable (Meslow 1993, Durbin 1996). This controversy intensified in 1988–1992, when a series of lawsuits by environmental groups halted all harvest of spotted owl habitat on federal lands (Dwyer 1989) and forced the U.S. Fish and Wildlife Service to list the northern spotted owl as a threatened subspecies (Zilly 1988, U.S. Fish and Wildlife Service 1990). The primary reasons given for listing the owl as threatened were that (1) habitat was declining, (2) there was evidence of declining populations, and (3) there were inadequate regulatory mechanisms to protect the owl or its habitat.

To meet the requirements of the National Forest Management Act and the Endangered Species Act, federal agencies in the Pacific Northwest adopted the Northwest Forest Plan (NWFP) in 1994. The NWFP was designed to protect habitat for spotted owls and other species associated with late-successional forests (Thomas et al. 1993) while allowing a reduced amount of commercial logging on federal lands (U.S. Department of Agriculture and U.S. Department of Interior 1994). The NWFP also placed large amounts of federal land within the range of the

northern spotted owl into riparian and late-successional forest reserves for which the primary objective was to maintain or restore habitat for spotted owls and other fish and wildlife species. Although the NWFP met the legal requirements for protection of spotted owls and other species associated with old forests, it has continued to be controversial. Some environmental groups argued that it was not adequate because it still allowed some harvest of old forests, whereas some industry groups argued that it was too extreme because it did not produce the expected levels of timber harvest on federal lands. Nonetheless, the controversy over management of spotted owls and old forests has led to an almost complete reversal of management objectives on federal forest lands in the Pacific Northwest. With the adoption of the NWFP, the primary focus of forest management on federal lands has shifted from timber production to maintaining biological diversity and ecological processes.

The controversy surrounding the spotted owl has led to considerable research on the species, including numerous studies of its distribution, population trends, habitat use, home range size, diet, prey ecology, genetics, dispersal, and physiology (for reviews, see Gutiérrez et al. 1995, Marcot and Thomas 1997, Noon and Franklin 2002). As a result, the spotted owl is one of the most intensively studied birds in the world. Despite this repository of knowledge, the effectiveness of current management plans for protecting the owl is still uncertain. This uncertainty has increased in recent years, as the barred owl has invaded the entire range of the northern spotted owl (Dunbar et al. 1991, Dark et al. 1998, Pearson and Livezey 2003) and appears to be affecting their territory occupancy (Kelly et al. 2003, Olson et al. 2005).

Most of the scientific and public debate about the northern spotted owl has focused on the degree to which the owl is negatively influenced by harvest of old forests (FEMAT 1993). To address this issue, the U.S. Forest Service, U.S. Bureau of Land Management, U.S. National Park Service, and nonfederal groups initiated several demographic studies on spotted owls from 1985 to 1990 (Appendix A). These long-term studies were designed to provide information on survival and fecundity rates of territorial owls that could then be used to estimate annual rates of population change (Forsman et al. 1996a, Lint et al. 1999). In 2003, there were 14 demographic studies being conducted on the northern spotted owl. Eight of these studies were part of the Monitoring Plan for the northern spotted owl under the NWFP (Lint et al. 1999). The other 6 were conducted by Indian tribes, timber companies, and private consulting firms.

Data from the demographic studies have been examined in 3 workshops since 1991, and the results have been reported in 4 documents (Anderson and Burnham 1992; Burnham et al. 1994, 1996; Franklin et al. 1999). Because of the contentious debate over management of spotted owls, participants in these workshops adopted formal protocols for error-checking data sets and selecting an a priori group of models for estimation of survival, fecundity, and annual rate of population change (Anderson et al. 1999). These protocols ensured that data were collected and prepared in a consistent manner among study areas and avoided the analyses of additional models after post hoc examination of results.

Subsequent to the analysis conducted by Franklin et al. (1999), we collected an additional 5 years of data from most of the demographic study areas. In January 2004, we conducted a workshop at Oregon State University and used a process similar to that used in previous analyses (Anderson et al. 1999) to update and analyze all the data. Our primary objectives were as follows:

1. estimate age-specific survival and fecundity rates and their sampling variances for territorial owls on individual study areas,
2. determine if there were any temporal trends in apparent survival or fecundity rates among study areas,
3. estimate annual rates of population change (λ) and their sampling variances for individual study areas and all study areas combined, and
4. compare the demographic performance of spotted owls on the 8 areas that are the basis of the Monitoring Plan for the NWFP (Lint et al. 1999) to that of owls on other areas.

The primary hypothesis that we were interested in testing was that the owl populations were stationary ($\lambda = 1.0$) as opposed to increasing ($\lambda > 1$) or declining ($\lambda < 1$) during the period of study. We also examined temporal trends in survival and fecundity rates, as increases or decreases in these rates could indicate fundamental changes in the dynamics of owl populations. We included 2 covariates in the analyses of temporal trends. First, the proportion of spotted owl territories with barred owl detections was used to test the hypothesis that barred owls had a negative effect on survival and fecundity of spotted owls. Second, we hypothesized that successful reproduction in 1 year had a negative effect on survival of adult owls the following year. In this paper, we describe the results of our analyses, including an assessment of the status and trends of northern spotted owl populations throughout most of the range of the subspecies.

STUDY AREAS

The 14 study areas included 4 in Washington: Wenatchee (WEN), Cle Elum (CLE), Rainier (RAI), and Olympic Peninsula (OLY); 6 in Oregon: Oregon Coast Ranges (COA), H. J. Andrews (HJA), Warm Springs Reservation (WSR), Tyee (TYE), Klamath (KLA), and southern Oregon Cascades (CAS); and 4 in California: Northwest California (NWC), Hoopa Tribal Area (HUP), Simpson Resource Area (SIM), and Marin (MAR) (Table 1; Fig. 1; Appendix A). The combined area of the 14 study areas was 28,430 km^2 (Table 1), which included about 12% of the 230,690-km^2 range of the northern spotted owl (U.S. Department of Agriculture and U.S. Department of Interior 1994). One study area (SIM) was entirely on private land, 2 (HUP, WSR) were on Indian Reservations, 5 (OLY, HJA,CAS, NWC, MAR) were primarily on federal lands, and 6 (CLE, WEN, RAI, COA, TYE, KLA) were characterized by a mixture of federal, private, and state lands (Fig. 1; Table 1). Study areas that were partly or entirely on lands administered by the U.S. Bureau of Land Management (BLM) typically included an ownership pattern in which 2.56-km^2 sections of BLM lands alternated with 2.56-km^2 sections of private land (KLA, TYE, COA, CAS).

Our study areas differed slightly from those in a previous analysis by Franklin et al. (1999) because 3 study areas were discontinued after 1998 (Astoria, Elliott State Forest, and East Eugene BLM) and 1 study (MAR) was started in 1998. We also modified the Olympic Peninsula Study Area to exclude nonfederal

Table 1. Descriptions of 14 study areas used to estimate vital rates of northern spotted owls in Washington, Oregon, and California (see also Appendix A). Asterisks indicate the 8 study areas that are part of the federal monitoring program for the owl (Lint et al. 1999).

| Study area | Area acronym | Years | Area (km²) | No. owls banded by age class[a] | | | | | No. captures/recaptures[b] |
				Juveniles	S1	S2	Adults	Total	
Washington									
Wenatchee	WEN	1990–2003	4,650	752	28	63	357	1,200	2,556
Cle Elum*	CLE	1989–2003	1,784	502	25	30	167	724	1,570
Rainier	RAI	1992–2003	2,133	97	8	7	105	217	530
Olympic Peninsula*	OLY	1987–2003	3,289	516	35	39	395	985	3,568
Oregon									
Coast Ranges*	COA	1990–2003	3,919	574	27	57	367	1,025	3,386
H. J. Andrews*	HJA	1987–2003	1,526	602	44	54	395	1,095	3,151
Warm Springs Reservation	WSR	1992–2003	1,001	233	10	13	125	381	867
Tyee*	TYE	1985–2003	1,741	610	67	63	292	1,032	3,293
Klamath*	KLA	1985–2003	1,384	698	98	73	278	1,147	2,964
South Cascades*	CAS	1991–2003	3,375	411	22	45	403	881	2,141
California									
NW California*	NWC	1985–2003	1,790	609	97	73	247	1,026	2,865
Hoopa Reservation	HUP	1992–2003	356	116	24	30	109	279	851
Simpson	SIM	1990–2003	1,265	708	80	127	429	1,344	4,087
Marin	MAR	1998–2003	217	41	9	10	36	96	225
Totals	—		28,430	6,469	574	684	3,705	11,432	32,054

[a] Age class codes indicate owls that were 1 year old (S1), 2 years old (S2), or ≥3 years old (adults).
[b] All captures and recaptures, regardless of age.

lands that were included in the previous analysis; we did this to distinguish population trends of owls on federal lands on the Olympic Peninsula from trends on nonfederal lands. Eight study areas (CLE, OLY, HJA, COA, TYE, KLA, CAS, NWC) were established by the U.S. Forest Service and BLM to monitor population trends of the northern spotted owl (hereafter referred to as the 8 monitoring areas) under the NWFP (Table 1; Appendix A; Lint et al. 1999).

All study areas were characterized by mountainous terrain, but there was great variation in topography among them. Study areas in coastal regions of western Oregon and northern California were in areas where elevations rarely exceeded 1,250 m and where forest vegetation generally extended from the lowest valleys to the highest ridges. In contrast, study areas in the Cascades Ranges and Olympic Peninsula typically included larger mountains, with the highest peaks and ridges extending well above timberline. Climate and precipitation were highly variable among areas, ranging from relatively warm and dry conditions on study areas in southern Oregon (CAS, KLA) and northern California (NWC, HUP) to temperate rain forests on the west side of the Olympic Peninsula (OLY), where precipitation ranged from 280 to 460 cm/year. Study areas on the east slope of the Cascades (WEN, CLE, WSR) were generally characterized by warm dry summers and cool winters, with most precipitation occurring as snow during winter.

Vegetation generally consisted of forests dominated by conifers or mixtures of conifers and hardwoods (Franklin and Dyrness 1973, Küchler 1977). Forests on study areas in Washington and Oregon were mostly characterized by mixtures of Douglas-fir and western hemlock (*Tsuga heterophylla*) or by mixed-conifer associations of Douglas-fir, grand fir (*Abies grandis*), western white pine (*Pinus monticola*), and ponderosa pine (*P. ponderosa*). Incense cedar (*Libocedrus decurrens*) was a common associate of mixed-conifer forests in Oregon. Forests on study areas in southwest Oregon and northern California were mostly mixed-

conifer or mixed-evergreen associations. In mixed-evergreen forests, evergreen hardwoods such as tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), California laurel (*Umbellularia californica*), and canyon live-oak (*Quercus chrysolepis*) formed a major part of the forest canopy, usually in association with Douglas-fir. The Simpson and Marin study areas in California also included large areas dominated by coastal redwoods (*Sequoia sempervirens*) and evergreen hardwoods.

Forest condition was highly variable among study areas ranging from mostly young forests (<60 years old) on 1 study area (SIM) to some study areas on federal lands (OLY, HJA, MAR, NWC, CAS) where >60% of the landscape was covered by mature (80–200 years old) or old-growth (>200 years) forests, as described by Thomas et al. (1990). Although the types and amounts of disturbance varied among areas, all study areas were characterized by a diverse mixture of forest seral stages that were the result of historic patterns of logging, wildfire, windstorms, disease, and insect infestations. On some study areas (OLY, RAI), forest cover was also naturally fragmented by high-elevation ridges covered by snow, ice, and alpine tundra.

Selection of study areas by the groups that participated in the analyses was based on many considerations, including forest type, logistics, funding, and landownership boundaries. As a result, study areas were not randomly selected or systematically spaced. Nevertheless, the amount of spotted owl habitat in the study areas was very similar (±5%) to that on surrounding federal lands for 9 of the 14 study areas (Appendix F). The study areas that were most different from the surrounding federal lands were national parks (OLY = +13%, MAR = +14%), tribal lands (HUP = −15%), or private lands (SIM = +14%), where these differences were expected because of past management strategies. Consequently, we believe that habitat conditions and owl population trends on the study areas were broadly representative of conditions on federal lands. Because coverage of state and private lands was
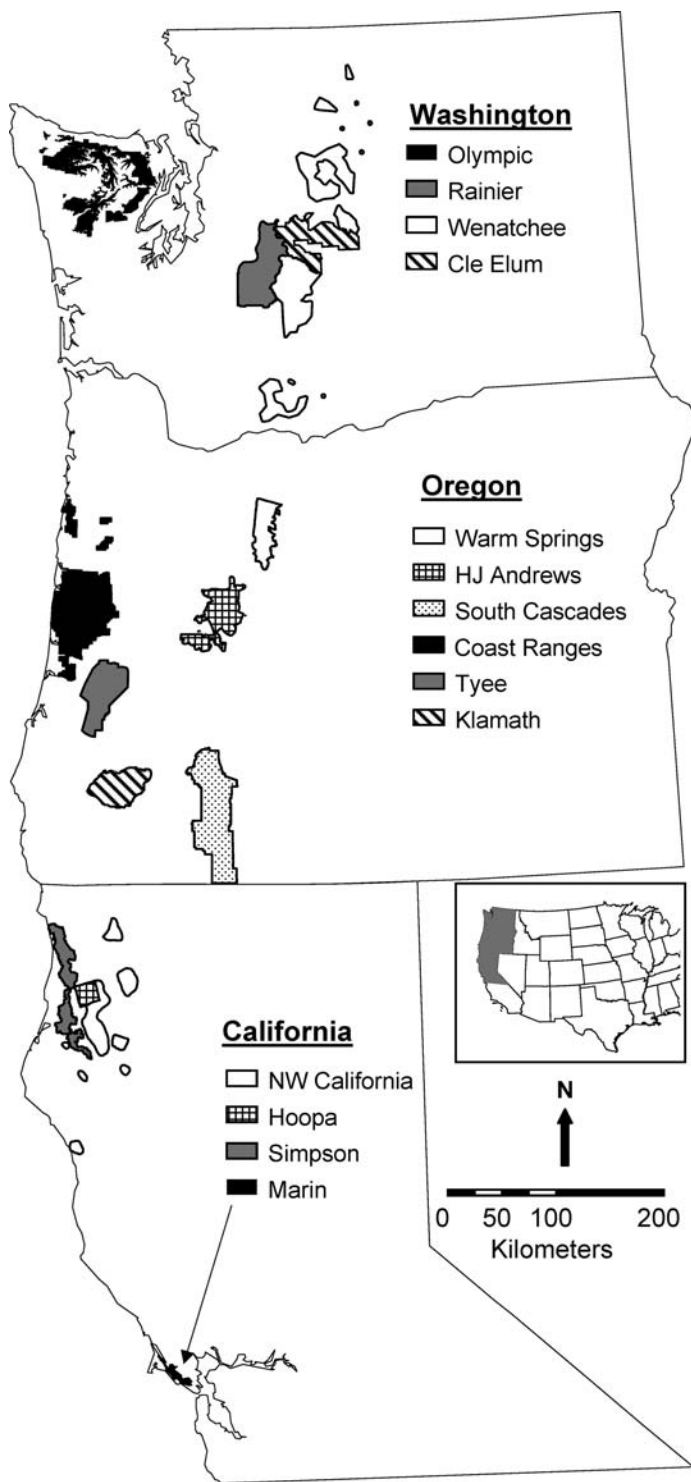
Figure 1. Location and distribution of the 14 study areas where we studied the demographic rates of northern spotted owls in Washington, Oregon, and California.

less extensive and management practices there varied widely, our results likely were not applicable to all state and private lands.

METHODS

Data Analysis

The demographic parameters of interest in our analyses were age-specific survival probabilities (ϕ), age-specific fecundity (b),

and annual rate of population change (λ). Data sets from each study area included a complete capture history of each owl banded during the study. Data were coded with sex and age (S1 = 1–2 years old, S2 = 2–3 years old, A = adult, S1 + S2 + A = nonjuveniles) of owls when they were first banded. We estimated reproductive output as the number of young fledged (NYF) by each territorial female located each year. We estimated annual rate of population change (λ) from a file that included the sex, age, and capture histories of all territorial owls that met certain criteria (see Annual Rate of Population Change below). Prior to data analysis, we used an error-checking process similar to Franklin et al. (2004) to ensure that all data sets were accurate and formatted correctly.

Prior to analyzing data, we discussed and agreed on protocols for the analyses and developed a priori lists of models for estimation of survival (ϕ), fecundity (b), and annual rate of population change (λ). The a priori models were developed from biological hypotheses following the procedures described by Anderson et al. (1999). A priori models differed somewhat by response variable and whether the analyses were on the individual study areas or part of a meta-analysis of all study areas combined. In all analyses, we examined temporal variation with models that had constant (.), annual (t), linear (T), or quadratic (TT) time effects. We also included a barred owl covariate in the analyses of survival and fecundity because we predicted that presence of barred owls would have a negative effect on demographic rates of spotted owls (Kelly et al. 2003). The barred owl (BO) covariate was year-specific and was the proportion of spotted owl territories in which barred owls were detected each year on each study area (Appendix B). Although we recognized that the impacts of barred owls were more likely to occur at the territory level, the only data that were available for all study areas was the year-specific covariate. Thus, we included the barred owl covariate as an exploratory variable to determine if the effects were detectable at this coarser scale. For the meta-analysis of apparent survival, we also included a covariate for the potential effect of reproduction (r) on survival during the following year. We used the mean NYF on each study area per occupied territory per year to model this effect. In all meta-analyses, we developed models that grouped study areas into larger categories related to ecological regions, ownership, or latitude (Appendix A).

We used estimates of regression coefficients (β) and their 95% confidence intervals as evidence of an effect on either fecundity or apparent survival by various factors or covariates. The sign of the coefficient represented a positive (+) or negative (−) effect of a factor or covariate, and the 95% confidence intervals were used to evaluate the evidence for $\beta < 0.0$ (negative effect) or $\beta > 0.0$ (positive effect). We used 95% confidence intervals as a descriptive measure of precision; however, we warn against improperly using such intervals as a dichotomous test to "reject" or "fail to reject" hypotheses based on a parameter estimate being outside or inside the interval, respectively.

Fecundity

Study areas were surveyed 3 times each year to locate owls, confirm bands, and band unmarked owls. All owls were marked with U.S. Fish and Wildlife Service bands and unique color bands that could be observed without recapturing owls (Forsman et al. 1996b, Franklin et al. 1996, Lint et al. 1999, Reid et al. 1999). If

owls were located on any of the 3 visits, field personnel followed a standard protocol to determine the nesting status and NYF by each territorial female (Lint et al. 1999). This protocol takes advantage of the fact that spotted owls are unafraid of humans and will readily take live mice from human observers. On capturing a mouse, a spotted owl that is nesting will usually carry the mouse directly to its nest or young. Owls that are not nesting or that have failed to produce young will simply eat or cache the mice. The standard protocol required that owls be located and offered at least 4 mice on 2 or more occasions each year to document their nesting status and the number of young produced. If the owls ate or cached all the mice on each occasion, then they were considered to be either nonnesting or failed nesters and received a score of "0" for the number of young produced. If owls carried mice to a nest or to fledged young, then the number of young fledged was recorded as the maximum number of young observed on either of 2 visits. On each of these 2 visits, the adults were offered 4 mice and followed as they carried the mice to their fledglings. On these occasions, it was usually possible to unambiguously determine the number of young in each brood by listening for the loud begging calls of the juveniles and watching as the adults fed them. The protocol included some exceptions that were adopted to reduce bias in fecundity estimates. For example, females were given a "0" for reproductive output if they (1) appeared to be nonnesting based on 1 or more visits during the early nesting season and could not be relocated on repeated visits or (2) were determined to be nesting and could not be relocated on repeated visits to the area. These exceptions were adopted because owls that did not nest or failed to produce young sometimes disappeared before the full protocol could be met, and excluding these individuals from the analysis would have caused a positive bias in fecundity. The protocol also included some exceptions that were designed to minimize the number of mice fed to owls. For example, under some conditions it was permissible to offer owls fewer than 4 mice if the behavior of owls clearly indicated that they were or were not nesting. Owls that did not meet the above protocols were excluded from the analysis and were recorded as "missing data" regardless of how many times they were located in a given year. For more details on this protocol, readers should consult Lint et al. (1999).

We conducted analyses on NYF per territorial female or nest (also referred to as productivity), but to be consistent with previous analyses of spotted owl demography (Forsman et al. 1996a, Franklin et al. 2004) results are reported as fecundity (no. females produced per territorial female). We estimated fecundity as NYF/2, assuming a 1:1 sex ratio of young produced at birth. Our assumption of a 1:1 sex ratio was based on a sample of juveniles that were sexed from genetic analysis of blood samples (Fleming et al. 1996, Fleming and Forsman, unpublished data). We assumed that the owls sampled were a representative sample of the owls in each age class and that sampling was not biased toward birds that reproduced. We believe these assumptions were reasonable because spotted owls usually remain on the same territories year-round and usually can be located even in years when they do not reproduce.

Fecundity on Individual Study Areas.—We used PROC MIXED in SAS (SAS Institute 1997) to fit a suite of models for each study area that included (1) the effects of age (a), (2) linear or quadratic time trends, (3) the proportion of spotted owl territories where barred owls were detected each year on each study area (BO covariate; see Appendix B), and (4) an even-odd year effect (EO). We included the even-odd year effect because a previous analysis (Franklin et al. 1999) suggested a cyclic biennial pattern to the number of young fledged, with higher reproductive rates in even-numbered years compared to odd-numbered years. A full set of models was developed for each study area before analyses began. Model ranking and selection of best models within study areas were based on minimum AIC_c (Burnham and Anderson 2002).

A plot of the annual variance-to-mean ratio for all study areas indicated that the variance of NYF was nearly proportional to the mean of NYF with some evidence of a reduction in variance at higher levels of reproduction. This plot was consistent with a truncated Poisson distribution (Evans et al. 1993), with owls seldom raising more than 2 young. As in Franklin et al. (1996), the average number of young fledged per age class in each study area and each year was first computed. Despite the integer nature of the underlying data (0, 1, 2, and rarely 3 young fledged), these data were not distributed as Poisson (Franklin et al. 1999, 2000). For this reason, we did not use Poisson regression, which is not robust to departures from a Poisson distribution (White and Bennets 1996). Thus, we used regression models based on the normal distribution, which are less biased. We also relied on the fact that the sample sizes were sufficiently large to justify the assumption of a normal distribution for each average as long as allowance was made for the dependence of the variation on the mean (see next paragraph). This averaging process also removed any ambiguity in the definition of the sampling unit for the analysis, as the appropriate unit of analysis is not the individual owl but the study area–age class combination, which responds to yearly effects that influence the entire study area. Issues of autocorrelation in the NYF over time for a particular territory are also avoided by treating study areas as the sampling unit. Consequently, we used the normal regression model on the averages for the analyses of NYF.

We also reduced the effect of the variance-to-mean relationship by fitting models to the yearly mean NYF by age class. These means for each study area were modeled as

PROC MIXED; MODEL MEAN_NYF $= fixed\ effects.$

Thus, residual variation was a combination of year-to-year variation in the actual mean and variation estimated around the actual mean and is approximately equal to

$$var(residual) = var(year\ effects) + var(NYF)/n,$$

where $n =$ the number of territorial females checked in a particular year. We thought this approach was justified for a number of reasons. First, a variance components analysis on the raw data comparing spatial variance among territories to temporal variance among years showed the former to be small relative to the latter and other residual effects (see Results). Therefore, we concluded that ignoring spatial variance within study areas would not bias the results, negating the need to include territory as a random effect. Second, we were able to support the key assumption that the var(residual) was relatively constant because (1) var(NYF)/n

was small relative to var(year effects), (2) the total number of female owls sampled was roughly constant over time for each study area so that var(NYF)/n was roughly constant, and (3) fewer measurements were taken on subadult owls such that var(NYF)/n was also about constant even though var(NYF) may decline with increasing age class. These assumptions were verified by Levine's test for homogeneity of variances. Third, we assumed that residual effects were approximately normally distributed because, based on the central limit theorem, the average of the measurements will have an approximate normal distribution with large sample sizes even if the individual measurements are discrete. Finally, covariates that were included in analyses of each study area (such as BO) were more easily modeled.

Because there was no consistent pattern to the best-fitting model among study areas, we used a nonparametric approach to estimate the mean NYF. First, the mean NYF was computed for each year and age class, then these averages were averaged across years within each age class. The estimated standard error was computed as the standard error of the average of the averages among years. This method gave equal weight to all years regardless of the number of birds actually measured in a year, and it did not force a model for changes over time. Essentially, it treated years as random effects with year effects being large relative to within-year sampling variation. Estimates weighted by sample sizes in each year were not substantially different.

Meta-analysis of Fecundity on All Study Areas.—We performed 2 meta-analyses of NYF data. In one analysis, we used all 14 study areas, and in the other we used the 8 monitoring areas (Lint et al. 1999). In both analyses, we used data from adult females only because samples of 1- and 2-year-old owls were small. In addition, we analyzed NYF for the same geographic regions and ownership categories used for the meta-analyses of survival and λ_{RJS} (Appendix A).

We used mixed models to perform meta-analyses on mean NYF per year for the same reasons specified above for the study area analyses. A particular region*year treatment combination was defined for each study area with owls within study areas as units of measure. Thus, the sampling units were study areas within region*year, which we treated as a random effect in the mixed models. As ownership and ecological region apply at the study area level rather than at the bird level, model selection was performed on average NYF by study area and year. We evaluated models that allowed for effects of ownership, geographic region, even-odd years, barred owls, linear and quadratic time trends, and variable time effects. Model rankings and selection of best models were based on minimum AIC$_c$ (Burnham and Anderson 2002).

Estimation of Apparent Survival

We used Cormack–Jolly–Seber open population models (Cormack 1964, Jolly 1965, Seber 1965, Burnham et al. 1987, Pollock et al. 1990, Franklin et al. 1996) in Program MARK (White and Burnham 1999) to estimate apparent survival of owls for each year (roughly from 15 June to 15 June). Owls that were not banded as juveniles were assigned to age classes based on plumage attributes (Forsman 1983, Moen et al. 1991, Franklin et al. 1996). We did not estimate juvenile survival rates because these estimates were confounded by emigration (Burnham et al. 1996, Forsman et al. 2002). In contrast, annual site fidelity of territorial owls was high

(Forsman et al. 2002), so emigration was not a serious bias in survival estimates from territorial owls.

We used capture–recapture data to estimate recapture probabilities (p, the probability that an owl alive in year t is recaptured, given that it is alive at the beginning of year t) and annual apparent survival probabilities (ϕ, the probability that an owl survives from time t to $t + 1$, given that it is alive at the beginning of year t). Our general approach for estimating survival rates was to (1) develop a priori models for analysis, (2) evaluate goodness of fit and estimate an overdispersion parameter ($\hat{c}$) for each data set, (3) estimate recapture probabilities and apparent survival for each capture–recapture data set with the models developed in step 1 using Program MARK (White and Burnham 1999), (4) adjust the covariance matrices and AIC$_c$ values with $\hat{c}$ to obtain QAIC$_c$ values, and (5) select the most parsimonious model for inference based on QAIC$_c$ model selection (Burnham and Anderson 2002). Additional details on methods of estimation of survival from capture–recapture data from northern spotted owls are provided by Burnham et al. (1994, 1996) and Franklin et al. (1996). Statistical analyses were based on maximum likelihood methods (Brownie et al. 1978, Burnham et al. 1987) and current philosophy of parametric statistical analysis of large, interrelated data sets (Anderson et al. 1999).

The goal of the data analysis and model selection process was to find a model from an a priori list of models that best fit the data and was closest to the truth based on Kullback–Leibler information (Burnham and Anderson 2002). Prior to model fitting, we used the global model {ϕ(s*t), p(s*t)} for adults to test each data set for goodness of fit to the assumptions of the Cormack–Jolly–Seber model. The global model included estimates of sex (s) and time (t) effects, plus the interaction between sex and time for both ϕ and p. We used Program RELEASE (Burnham et al. 1987) to test for goodness of fit to the Cormack–Jolly–Seber model and estimate overdispersion. Overdispersion in the data was estimated by $\hat{c} = \chi^2/$df using the combined χ^2 values and degrees of freedom (df) from tests 2 and 3 in Program RELEASE (Burnham et al. 1987). Estimates of $\hat{c}$ were used to inflate standard errors and adjust for the lack of independence in the data. We estimated recapture probabilities and apparent survival with 56 a priori models that were developed during the protocol session (Tables 2, 3). Models, which included age, sex, time, time trends (linear and quadratic), and a barred owl covariate (Appendix B), were then fit to each data set to model apparent survival (Table 3).

We used maximum likelihood estimation in Program MARK (White and Burnham 1999) to fit models and optimize parameter estimation. We used QAIC$_c$ for model selection (Lebreton et al. 1992, Burnham and Anderson 2002), which is a version of Akaike's information criterion (Akaike 1973, 1985; Sakamoto et al. 1986) corrected for small sample bias (Hurvich and Tsai 1989) and overdispersion (Lebreton et al. 1992, Anderson et al. 1994). We computed QAIC$_c$ for each candidate model and selected the best model for inference based on the minimum QAIC$_c$ value (Burnham and Anderson 2002:66–70). Two additional tools based on QAIC$_c$ values were also computed for each model, ΔQAIC$_c$ for model i (where ΔQAIC$_{ci}$ = QAIC$_{ci}$ − minQAIC$_c$) and Akaike weights (Buckland et al. 1997, Burnham and Anderson 2002).

Table 2. A priori models used for analysis of recapture probabilities (*p*) of northern spotted owls on 14 demographic study areas in Washington, Oregon, and California. φ structure for all models was φ(a*s*t).

Model[a]	Description of *p* structure
1. *p*(a*s*t)	Age, sex, and time effects with all interactions (global model)
2. *p*(.)	Constant model (no effects)
3. *p*(s)	Sex effect
4. *p*(r)	Effect of annual reproduction on *p* in following year
5. *p*(r + s)	Additive reproduction and sex effects
6. *p*(t)	Annual time effect
7. *p*(s + t)	Additive sex and time effects
8. *p*(T)	Linear time trend effect
9. *p*(s + T)	Additive sex and linear time trend effects
10. *p*(BO)	Barred owl effect
11. *p*(s + BO)	Additive sex and barred owl effects
12. *p*(s + BO + r)	Additive sex, barred owl, and reproduction effects
13. *p*(choice)	Biologist's choice[b]

[a] Model notation indicates structure for effects of age (a), sex (s), annual time (t), linear time trend (T), reproduction (r), barred owls (BO), or biologist's choice (choice). Age structure included 3 age classes (1 year old, 2 years old, and ≥3 years old).
[b] Up to 3 additional models of choice that incorporated potential area-specific effects on *p* (i.e., survey effort, study area subregions, survey method).

Table 3. A priori models used for analysis of apparent survival (φ) of northern spotted owls on 14 demographic study areas in Washington, Oregon, and California. Analyses used the best *p* structure from the initial analysis for each study area.

Model[a]	Description of φ structure
1. φ(S1 = S2 = A)	Constant φ, no age, sex, or time effects
2. φ([S1 = S2 = A] + s)	Sex effect only
3. φ(S1, S2 = A)	Age effect (S2 = A, S1 different)
4. φ([S1, S2 = A] + s)	Age effect (S2 = A, S1 different), additive sex effect (s)
5. φ(S1 = S2, A)	Age effect (S1 = S2, A different)
6. φ([S1 = S2, A] + s)	Age effect (S1 = S2, A different), additive sex effect (s)
7. φ(S1, S2, A)	Age effect (all age classes different)
8. φ([S1, S2, A] + s)	Age effect (all age classes different), additive sex effect (s)
9. φ(models 1–8 + t)	Minimum QAIC model from 1–8 above with additive time effect (t)
10. φ(models 1–8 + T)	Minimum QAIC model from 1–8 above with additive linear time effect (T)
11. φ(models 1–8*T)	Minimum QAIC model from 1–8 above with interactive linear time effect (T)
12. φ(models 1–8 + TT)	Minimum QAIC model from 1–8 above with additive quadratic time effect (TT)
13. φ(models 1–8*TT)	Minimum QAIC model from 1–8 above with interactive quadratic time effect (TT)
14. φ(models 1–8 + BO)	Minimum QAIC model from 1–8 above with additive barred owl effect (BO)

[a] Model notation indicates structure for effects of age (S1, S2, A), sex (s), annual time (t), linear time trend (T), or quadratic time trend (TT). Age classes (S1, S2, A) indicate owls that were 1, 2, or ≥3 years old, respectively. Symbols separating age classes indicate if they were combined (=) or estimated separately (,).

Akaike weights were used to address model selection uncertainty and the degree to which ranked models were considered competitive. We used Akaike weights to compute estimates of time-specific, model-averaged survival rates and their standard errors for each study area (Burnham and Anderson 2002:162). We did this because there were often several competitive ($\Delta QAIC_c < 2.0$) models for a given data set (Burnham and Anderson 2002).

For each study area, we used the variance components module of program MARK to estimate temporal ($\sigma^2_{temporal}$) process variation (Burnham and White 2002, White et al. 2002). This approach allowed us to separate sampling variation (variation attributable to estimating a parameter from a sample) in apparent survival estimates from total process variation. Process variation was decomposed into temporal (parameter variation over time) and spatial (parameter variation among different locations) components.

Meta-analysis of Apparent Survival.—The meta-analysis of apparent survival was based on capture histories of adult males and females from the 14 study areas. Apparent survival and capture probabilities were estimated with the Cormack–Jolly–Seber model using Program MARK (White and Burnham 1999). The global model for these analyses was {φ(g*s*t) *p*(g*s*t)}, where g was study area, t was time (year), and s was sex. Goodness of fit was assessed with the global model in Program RELEASE (Burnham et al. 1987), and the estimate of overdispersion, *c*, was used to adjust model selection to QAIC and inflate variance estimates. We initially evaluated 6 models of recapture probability {*p*(g + t), *p*(r), *p*(g + s + t), *p*(r + s), *p*([g + t]*s), *p*(r*s)} with a general structure on apparent survival {φ(g*t*s)}, where r is the mean NYF per territorial female on each study area per year. Using the model for *p* with minimum QAIC from the initial 6 models, we evaluated 13 additional models for apparent survival to test for various combinations of area, sex, time, barred owl effects (BO covariate; Appendix B), and effects of reproductive output (r) (Table 4). The

sex effect was then removed from the best model above to check for strength of the sex effect. Then we ran 4 more models in which study area (group) effect was replaced with the group surrogates "ownership," "geographic region," "ownership*region," and "latitude" for a total of 27 models. Ownership referred to whether the area was privately owned, federally owned, or of mixed private and federal ownership (Appendix A). Each study area was classified into 1 of 6 geographic regions that incorporated geographic location and the major forest type in the study area (Appendix A). Latitude was a continuous variable measured at the center of each study area.

Annual Rate of Population Change (λ)

One of the first topics we discussed during the workshop was whether we should estimate the annual rate of population change (λ) from estimates of age-specific survival and fecundity with the Leslie projection matrix (λ_{PM}) (Caswell 2000) or the reparameterized Jolly–Seber method (λ_{RJS}) (Pradel 1996). The λ_{PM} method was used in the 1993 and 1998 demographic analyses of northern spotted owls (Franklin et al. 1996, 1999). The λ_{RJS} method, which uses direct estimation of λ from capture–recapture data, was used in an exploratory manner in the 1998 analyses (Franklin et al. 1999) and was used by Franklin et al. (2004) to analyze data from California spotted owls (*S. o. occidentalis*).

Estimates of λ_{PM} are computed from projection matrices using age-specific survival and fecundity for juvenile, subadult, and adult owls, assuming a stable age distribution (i.e., constant rates over time) over the period of study. The estimate of λ_{PM} represents the

Table 4. A priori models used for meta-analysis of apparent survival (ϕ) and recapture probabilities (p) of adult female northern spotted owls on 14 study areas in Washington, Oregon, and California.

Model[a]	Description of model structure
1. $\phi(g*t*s)$ $p(g*t*s)$	ϕ(area, time, and sex effects with all interactions): p(area, time, and sex effects with all interactions)
2. $\phi([g*t] + s)$ $p(g + t)$	ϕ(area and time effects with interactions, plus additive sex effect): p(additive area and time effects)
3. $\phi([g*t] + s)$ $p(g + s + t)$	ϕ(area and time effects with interactions, plus additive sex effect): p(additive area, sex, and time effects)
4. $\phi([g*t] + s)$ $p([g + t]*s)$	ϕ(area and time effects with interactions, plus additive sex effect): p(additive area and time effects, interacting with sex)
5. $\phi([g*t] + s)$ $p(r)$	ϕ(area and time effects with interactions, plus additive sex effect): p(reproduction effect)
6. $\phi([g*t] + s)$ $p(r + s)$	ϕ(area and time effects with interactions, additive sex effect): p(additive reproduction and sex effects)
7. $\phi([g*t] + s)$ $p(r*s)$	ϕ(area and time effects with interactions, plus additive sex effect): p(reproduction and sex effects with interactions)
8. $\phi(g + s)$ p(best)	ϕ(additive area and sex effects): p(best p structure from models 2–7 above)
9. $\phi(g + s + t)$ p(best)	ϕ(additive area, sex and time effects): p(= model 8)
10. $\phi([g*T] + s)$ p(best)	ϕ(area and linear time effects with interactions, plus additive sex effect): p(= model 8)
11. $\phi(g + T + s)$ p(best)	ϕ(additive area, linear time trend, and sex effects): p(= model 8)
12. $\phi([g*TT] + s)$ p(best)	ϕ(area and quadratic time effects with interactions, plus additive sex effect): p(= model 8)
13. $\phi(g + s + TT)$ p(best)	ϕ(additive area, sex, and quadratic time effects): p(= model 8)
14. $\phi(s + t)$ p(best)	ϕ(additive sex and time effects): p(= model 8)
15. $\phi(s + TT)$ p(best)	ϕ(additive sex and quadratic time effects): p(= model 8)
16. $\phi(s + T)$ p(best)	ϕ(additive sex and linear time effects): p(= model 8)
17. $\phi(s)$ p(best)	ϕ(sex effect): p(= model 8)
18. $\phi(BO + s)$ p(best)	ϕ(additive barred owl and sex effects): p(= model 8)
19. $\phi(g + BO + s)$ p(best)	ϕ(additive area, barred owl, and sex effects): p(= model 8)
20. $\phi([g*BO] + s)$ p(best)	ϕ(area and barred owl effects with interactions, plus additive sex effect): p(= model 8)
21. ϕ(no sex) p(best)	ϕ(lowest QAIC$_c$ model from models 8–20 with sex effect removed): p(= model 8)
22. ϕ(owner) p(best)	ϕ(replace area effect in lowest QAIC$_c$ model from models 8–21 with ownership effect): p(= model 8)
23. ϕ(region) p(best)	ϕ(replace area effect in lowest QAIC$_c$ model from models 8–21 with region effect): p(= model 8)
24. ϕ(owner*region) p(best)	ϕ(replace area effect in lowest QAIC$_c$ model from models 8–21 with ownership and region effects with interactions): p(= model 8)
25. ϕ(best + latitude) p(best)	ϕ(additive latitude effect with best area effect model from models 8–24): p(= model 8)

[a] Model notation indicates structure for effects of study area (g), annual time (t), linear time trend (T), quadratic time trend (TT), geographic region (region), landownership (owner), latitude, or barred owls (BO).

asymptotic growth rate of a population with constant demographic rates over time, but it is not necessarily the best estimate of annual rate of population change for several reasons. First, there is asymmetry in the way movement is treated in vital rates representing gains or losses. In demographic studies of spotted owls, apparent survival rates are estimated using capture–recapture models, whereas fecundity rates are estimated from direct observation of productivity of territorial females. Population losses thus include both death and permanent emigration, whereas gains come solely from reproduction, as reflected by fecundity estimates. Second, λ_{PM} is an asymptotic value expected to result from the absence of temporal variation in the vital rates, whereas we know from previous analyses (Burnham et al. 1996, Franklin et al. 1999) that there is considerable temporal variation in both survival and fecundity of spotted owls. Thus, λ_{PM} is a theoretical, asymptotic rate assuming constant fecundity and survival rates over the period of study, whereas λ_{RJS} is an estimate of a rate that reflects annual variability in rates of population change. Third, values of fecundity may be positively biased if nonbreeders or unsuccessful breeders are not detected as readily as successful breeders (Raphael et al. 1996). Finally and most important, estimates of juvenile survival are negatively biased because of permanent emigration from study areas, which is of paramount concern for northern spotted owls (Franklin et al. 2004, Boyce et al. 2005). The Cormack–Jolly–Seber estimates of apparent survival cannot distinguish between undetected emigrants and individuals that have died. To the extent that banded juveniles (or nonjuveniles) emigrate from study areas, survive at least 1 year, and are never observed again, the estimates of survival will be negatively biased. As a result,

estimates of λ_{PM} will be biased low (Raphael et al. 1996, Franklin et al. 2004). The strength of the λ_{RJS} method is that it takes into account the combination of gains and losses to the population by direct estimation from the capture history of individual owls and their recapture probabilities. Also, the interpretation of λ_{RJS} as a rate of change in the number of territorial owls on the study is clear and unambiguous. Because of these reasons, the λ_{RJS} method is much preferred over the λ_{PM} method to estimate annual rates of population change for spotted owls (Franklin et al. 2004, Boyce et al. 2005).

Pradel (1996) introduced a reparameterization of the Jolly–Seber model permitting estimation of λ_t, the finite rate of population increase [defined by N_{t+1}/N_t, where N_t represents population size at time t] in addition to apparent survival (ϕ) and recapture probability (p). We used this method to estimate λ_{RJS} and determine whether populations were increasing ($\lambda > 1.0$), decreasing ($\lambda < 1.0$), or stationary ($\lambda = 1.0$). Annual rates of population change, λ_t, were estimated directly from capture history data for territorial owls from areas that were consistently surveyed each year (Pradel 1996). For models that had a variable time structure (t) on λ, we used a random-effects model to estimate λ_t and its standard error. In addition to the ability to obtain time-specific estimates of λ_{RJS}, the models implemented in Program MARK also allowed for constraints, such as linear (T) or quadratic (TT) time effects on λ_{RJS}.

Estimates of λ_{RJS} reflect changes in population size resulting from reproduction, mortality, and movement into and out of the study areas. The data used in the analyses included only territorial individuals of mixed age classes (e.g., 1- and 2-year-olds and

adults combined). Thus, estimates of λ_{RJS} from any particular capture–recapture data set should correspond to changes in the territorial population within the area sampled. Gains in the territorial population can result from recruitment of owls born on the study area and from immigration of owls from outside the study area. Losses in the population result from mortality or emigration from the study area. To apply this method correctly, it is critical that the area sampled remains constant from year to year, coverage of the area is reasonably constant each year, and all areas or territories in the initial sample be visited during each subsequent year of study, regardless of recent occupancy status (e.g., even if no owls were detected on sites for several consecutive years). Observers on all study areas followed a set of survey protocols to ensure that these conditions were met (Franklin et al. 1996). In our analyses, there were 2 kinds of data sets for territorial owls: those for which all of the area within a study area was surveyed each year (density study areas [DSAs]) and those for which specific owl territories within a large geographic region were surveyed each year (territorial study areas [TSAs]). The DSAs included TYE, NWC, HUP, and SIM, and TSAs included WEN, CLE, RAI, OLY, WRS, HJA, COA, KLA, CAS, and MAR. For both survey types, the interpretation of λ_{RJS} is the change in the number of territorial owls in the sampled area. We analyzed the data from DSAs and TSAs separately because the capture–recapture data were collected with different sampling protocols. We did not make direct comparisons of the λ_{RJS} from the 2 types of surveys because DSAs were mostly in the southern part of the owl's range and TSAs in the northern portion; therefore, survey type and geographic area were confounded.

Annual Rate of Population Change for Individual Study Areas.—Although most areas sampled in TSAs were initially selected because they were occupied by owls or had been occupied by owls prior to the study, any bias toward occupied sites in early years of the study was largely eliminated by removing the first 1–5 years of data from each TSA. For DSAs, the number of initial years removed from the analysis varied from 0 to 5, depending on how well the study areas were surveyed during the early years of the study (Appendix A). These adjustments were made to reduce any potential bias in estimates of λ associated with any artificial population growth attributable to the initial location and banding of owls that occurs in the first few years of a study. To evaluate whether study areas were initially saturated with territorial owls (i.e., were capable of population growth), we computed the proportion of territories in which owls were detected in the first year used to estimate λ_{RJS}. Mean estimates for the proportion of territories that were occupied the first year of estimation were 0.629 (range = 0.547–0.700) and 0.791 (range = 0.680–0.906) for DSAs and TSAs, respectively. This indicated there was room for population growth or decline for both types of survey areas. Once the data were truncated, boundaries of 8 study areas remained unchanged for the duration of the study, and 6 areas had a 1-time increase in the study area to include areas that were added to the sample after the study was initiated (Appendix A). In the latter cases, owl territories located after the initial year of study were brought into the sample in a single expansion year, with any data prior to the expansion year removed from the capture histories of the owls that occupied those territories. Thus, new territory

occupants added in the expansion year were not considered to be new recruits in that year, so they did not effect the estimates of λ.

To estimate $\bar{\lambda}_t$ (average λ_{RJS}) and λ_t (year-specific λ) for each study area, we used the random effects module in Program MARK (White et al. 2002). We fit 2 general λ_{RJS} models $\{(\phi(t)\ p(t)\ \lambda(t)\}$ and $\{\phi(s^*t)\ p(s^*t)\ \lambda(s^*t)\}$ to the area-specific data. In some cases, study areas were expanded midway through the time interval. In these cases, we used group-effect models $[\{\phi(g^*t)\ p(g^*t)\ \lambda(g^*t)\}$ and $\{\phi(g^*s^*t)\ p(g^*s^*t)\ \lambda(g^*s^*t)\}]$ to estimate parameters associated with preexpansion areas separately from those of postexpansion areas. Regardless of the global models used, we used $QAIC_c$ to choose the best of the initial models to proceed with the estimation of $\bar{\lambda}_t$ using the following random effects models: constant across time (λ.), a linear time trend (λ_T), and a quadratic time trend (λ_{TT}). We removed the first 2 and the last estimates of λ_t from the base model before we fit the 3 random effects models to the data. This was done to eliminate potential biases due to (1) a trap/capture response, (2) a learning curve often exhibited by field crews on a new study area, or (3) capture probabilities differing between marked and unmarked birds early in each study (Hines and Nichols 2002). As with the survival analysis, we estimated overdispersion (c) for the λ_{RJS} data using Program RELEASE and the global model $\{\phi(s^*t)\ p(s^*t)\ \lambda(s^*t)\}$ for each study area. Estimates of $\bar{\lambda}_t$ were generated from the best random effects model. In cases where a linear (T) or quadratic (TT) time trend on λ was supported, we used the beta estimates from the random effects model and the midpoint of the time period of the study as the independent variable to estimate average λ_{RJS}. Standard errors for these estimates were developed using the Taylor series (i.e., "delta method"). We used the variance components module in Program MARK to compute estimates of temporal process variation ($\sigma^2_{temporal}$) for λ_{RJS} on each study area (Burnham and White 2002, White et al. 2002).

Meta-analyses of Annual Rate of Population Change.—In addition to estimates of λ_{RJS} for each study area, we conducted 2 meta-analyses of λ_{RJS} in which we computed average estimates of λ_{RJS} for multiple study areas combined. One meta-analysis included the 10 TSAs, and the other included the 4 DSAs. We used similar procedures in both analyses. The meta-analysis of λ_t involved fitting models to data from 3 different groups of study areas. The first grouping treated each of the study areas separately. The second grouping aggregated study areas by ownership, and the third aggregated them by geographic region. For each of these groupings, 3 models for λ_t were fit to the data. Model $\{\phi(g^*t)\ p(g^*t)\ \lambda(g^*t)\}$ was the most general model, which included full study area by time interactions on all 3 parameters. Model $\{\phi(g^*t)\ p(g^*t)\ \lambda(g+t)\}$ represented the hypothesis that temporal variation in λ_t occurred in parallel among the different groups for shared years, suggesting similar responses of population growth to environmental factors. Model $\{\phi(g^*t)\ p(g^*t)\ \lambda(t)\}$ represented the hypothesis of no variation in λ_t among geographic regions. Model $\{\phi(g^*t)\ p(g^*t)\ \lambda(g)\}$ represented area-specific population growth that did not vary from year to year. We also included the model $\{\phi(g^*t)\ p(g^*t)\ \lambda(.)\}$ reflecting constant λ over areas and years. There were a total of 11 models fit to the data for each of the DSAs.

We attempted to fit the same models to the data from TSAs but the maximum likelihood estimates of λ would not converge under

Table 5. Estimates of age-specific fecundity (no. female young produced per female) of northern spotted owls on 14 study areas in Washington, Oregon, and California.

Study area[a]	Years	1-year-old owls			2-year-old owls			Adults (≥3 years old)		
		n[b]	$\bar{x}$	SE	n[b]	$\bar{x}$	SE	n[b]	$\bar{x}$	SE
Washington										
WEN	1990–2003	20	0.050	0.050	49	0.290	0.085	758	0.491	0.058
CLE	1989–2003	23	0.136	0.097	34	0.467	0.117	423	0.574	0.069
RAI	1992–2003	4	0.000	0.000	7	0.000	0.000	184	0.253	0.061
OLY	1987–2003	11	0.071	0.050	19	0.267	0.098	883	0.293	0.057
Oregon										
COA	1990–1992	17	0.000	0.000	53	0.111	0.045	1,168	0.260	0.050
HJA	1987–2003	22	0.109	0.091	35	0.113	0.060	1,026	0.321	0.045
WSR	1992–2003	7	0.000	0.000	16	0.311	0.110	303	0.424	0.070
TYE	1985–2003	72	0.054	0.032	90	0.201	0.047	973	0.319	0.040
KLA	1985–2003	69	0.070	0.028	103	0.285	0.052	795	0.445	0.040
CAS	1991–2003	26	0.061	0.046	42	0.223	0.082	780	0.377	0.059
California										
NWC	1985–2003	64	0.101	0.066	78	0.205	0.052	938	0.333	0.032
HUP	1992–2003	10	0.000	0.000	15	0.056	0.056	273	0.216	0.043
SIM	1990–2003	60	0.109	0.040	104	0.118	0.030	1,168	0.326	0.037
MAR	1998–2003	12	0.275	0.195	12	0.271	0.159	156	0.530	0.056
Total/mean		417	0.074	0.029	657	0.208	0.032	9,828	0.372	0.029

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Oregon Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] Sample size indicates the no. cases in which we sampled owls in each age class. This is not the sample that was used to calculate means and standard errors. Those estimates were based on the no. years in the survey period. Estimates were determined using a nonparametric approach.

models with many parameters. The most general model $\{\phi(g^*t)\ p(g^*t)\ \lambda(g^*t)\}$ could not be fit to the data using a single data structure. Instead, we obtained estimates for this model by fitting a model to each group separately. Goodness-of-fit and model selection statistics were obtained using results of these individual analyses. None of the models retaining the general structure (g^*t) on survival and capture parameters could be evaluated. Thus, we tried to fit models in which survival and capture parameters, as well as population growth rate, were grouped by ownership or by geographic region. Because of these numerical difficulties, our final results were limited to 5 models: $\{\phi(g^*t)\ p(g^*t)\ \lambda(g^*t)\}$, $\{\phi(owner^*t)\ p(owner^*t)\ \lambda(owner + t)\}$, $\{\phi(owner^*t)\ p(owner^*t)\ \lambda(owner^*t)$, $\{\phi(t)\ p(t)\ \lambda(t)\}$, and $\{\phi(region^*t)\ p(region^*t)\ \lambda(region + t)\}$.

Estimates of Realized Population Change.—We used the methods of Franklin et al. (2004) to convert estimates of λ_t into estimates of realized population change. Annual realized changes in populations were estimated and expressed relative to initial population size (i.e., in the initial year used for analysis). Thus, we focused on the ratio of the population size in year t to that in the initial year (i.e., $\Delta_t = N_t/N_x$, where x is the initial year). Consequently, estimates of realized change corresponded to the proportional change in the population over the time period for which the λs were estimated. Realized population change (Δ_t) was estimated as

$$\hat{\Delta}_t = \prod_{i=x}^{t-1} \hat{\lambda}_i$$

where x was the year of the first estimated λ_t. For example, if $\hat{\lambda}_t$ was 0.9, 1.2, and 0.7 for 3 time intervals, then $\hat{\Delta}_t$ would be computed as $(0.9)(1.2)(0.7) = 0.756$, indicating that the ending population was 75.6% of the size of the initial population. To

compute 95% confidence intervals for $\hat{\Delta}_t$, we used a parametric bootstrap algorithm with 1,000 simulations. Our approach was similar to that of Franklin et al. (2004) except that our 95% confidence intervals were based on the ith and jth values of Δ_t arranged in ascending order where $i = (0.025)(1,000)$ and $j = (0.975)(1,000)$.

RESULTS

Fecundity

Individual Study Areas.—Estimates of fecundity were based on 10,902 observations of the number of young produced by territorial females. Most fecundity data were from territories that were occupied by adult females, which reflects the low frequency of territory occupancy and breeding attempts by 1- or 2-year-old females (Table 5). For all areas, age was the primary factor that affected fecundity (Table 6). Mean fecundity was lowest for 1-year-old females ($\bar{x} = 0.074$, SE = 0.029), intermediate for 2-year-olds ($\bar{x} = 0.208$, SE = 0.032), and highest for adults ($\bar{x} = 0.372$, SE = 0.029). Fecundity of adult females was highest (>0.40) on the CLE, WEN, WSR, KLA, and MAR study areas, whereas fecundity was lowest (<0.30) on RAI, OLY, COA, and HUP (Table 5).

Among the individual study areas, the model that was most frequently selected as best ($n = 7$) was female age + an even-odd year effect (A + EO), indicating high fecundity in even-numbered years and low fecundity in odd-numbered years with parallel changes among age-groups (Fig. 2). This model also was within 2 AIC_c units of the best model for 3 other study areas (Table 6). The best models for 2 additional areas contained the similar effects: (A*EO) for RAI and (A + EO + TT) for HJA. Thus, age and the even-odd year effect were important in explaining variability in

fecundity for most areas despite some weakening of the latter effect in recent years (Fig. 2). The even-odd year pattern was most prevalent for adults during the 1990s. In the 3 areas for which EO was not an important factor, (A + T) was the top model for TYE and NWC, indicating linear changes in fecundity over time (see below). There were no factors (constant model) that affected fecundity on the MAR study area. The MAR study was initiated in 1998 about the time the even-odd year effect waned and had few owls in younger age classes, so it was not surprising that the simplest model was selected.

Our results indicate that changes in fecundity over the period of study were variable among study areas. Linear (T) or quadratic (TT) time trends were evident in the model selection results on 9 of the 14 study areas (Table 7). On 5 study areas (HJA, TYE, CAS, NWC, HUP), time trends were included in the best model, and on 4 areas (WEN, CLE, COA, SIM) time trends were in models <2 AIC$_c$ units from the best model. All these time effects on NYF were linear except for HJA, which was quadratic but stable overall. The time trends for 2 areas (TYE and HUP) were positive with $\hat{\beta} > 0.0$ (Table 7). In contrast, there was evidence for negative trends in fecundity on 6 study areas (WEN, CLE, COA, CAS, NWC, SIM) with the upper confidence intervals barely >0.0 (Table 7). Fecundity appeared to be stable over the period of study on the RAI, OLY, WSR, HJA, KLA, and MAR study areas.

The barred owl covariate (BO) was not a part of the best model structure for any of the study areas, but there were 9 study areas for which BO effects were included in competing (ΔAIC < 2.0) models (Table 8). Of these, 5 (WEN, OLY, COA, NWC, SIM) had a negative association between fecundity and barred owl presence, and 4 (TYE, KLA, HUP, MAR) had a positive relationship. Confidence intervals were generally large and most substantially overlapped 0.0 except for HUP and MAR, for which the relation was positive. Results for these 2 areas were suspect because barred owls were rare on both areas (detections on <5% of spotted owl territories) and because MAR had only 6 years of data. The northern study areas where barred owls were most common were not more likely to have competing models with the BO covariate; in fact, the reverse seemed to be true with 4 of 4 areas in California, 3 of 6 areas in Oregon, and 2 of 4 areas in Washington having BO in models within 2 AIC$_c$ units of the best model (Table 8). The best BO model for CLE, thought to be the area most affected by barred owl encroachment, was >2.5 AIC$_c$ units from the best model. In summary, we were unable to show any negative effects of barred owls on spotted owl fecundity with the time-specific BO covariate.

Variance Component Analysis.—Estimation of spatial (site to site), temporal (year to year), and residual variance on the territory-specific data indicated that spatial and temporal variance within all study areas was low relative to the other variance components (Table 9). With the exception of MAR, for which spatial variance was 12% of the total variability in NYF, spatial variability within all study areas was <8%. Temporal variation in NYF ranged from 0.054 to 0.227 but never accounted for >30% of the total variability. The largest proportion of temporal variation occurred in the data from OLY and CLE (28 and 23%, respectively), but the temporal variation for the other study areas in Washington was not greater than that for the 6 study

Table 6. Best model and competing models with Δ$_i$ < 2.0, from the analysis of the number of young fledged (NYF) by female northern spotted owls on 14 study areas in Washington, Oregon, and California.

Study area and models[a]	−2log$\mathscr{L}$	K[b]	AIC$_c$	ΔAIC$_c$[c]	Akaike weight
Washington					
Wenatchee (WEN)					
A + EO	35.30	5	47.37	0.00	0.31
A + EO + BO	33.55	6	48.55	1.18	0.17
A + EO + T	33.70	6	48.70	1.33	0.16
Cle Elum (CLE)					
A + EO	74.94	5	86.70	0.00	0.36
A + EO + T	72.46	6	87.01	0.31	0.31
Rainier (RAI)					
A*EO	−20.18	7	3.16	0.00	0.89
Olympic (OLY)					
A + EO	21.60	5	34.00	0.00	0.55
A + EO + BO	20.25	6	35.75	1.74	0.23
Oregon					
Coast Range (COA)					
A + EO	2.50	5	14.81	0.00	0.43
A + EO + T	0.98	6	16.34	1.53	0.20
A + EO + BO	1.35	6	16.71	1.91	0.16
H. J. Andrews (HJA)					
A + EO + TT	26.92	7	44.42	0.00	0.89
Warm Springs (WSR)					
A	25.08	4	35.58	0.00	0.36
A + EO	22.71	5	36.71	1.13	0.20
Constant	32.57	2	37.23	1.66	0.16
Tyee (TYE)					
A + T	27.31	5	38.62	0.00	0.31
A	30.80	4	39.65	1.03	0.18
A + BO	29.23	5	40.53	1.92	0.12
Klamath (KLA)					
A + EO	30.20	5	41.59	0.00	0.22
A	32.73	4	41.64	0.05	0.22
A*EO	26.69	7	43.42	1.83	0.09
A + BO	32.07	5	43.47	1.88	0.09
S. Cascades (CAS)					
A + EO + T	31.92	6	46.72	0.00	0.36
A + EO	35.84	5	47.78	1.06	0.21
A + EO + TT	30.85	7	48.71	1.99	0.13
California					
NW California (NWC)					
A + T	51.40	5	62.68	0.00	0.27
A + BO	52.66	5	63.93	1.25	0.14
A	55.22	4	64.05	1.37	0.13
A + TT	50.30	6	64.13	1.45	0.13
Hoopa (HUP)					
A + EO + T	−7.99	6	7.83	0.00	0.32
A + EO + BO	−7.47	6	8.35	0.53	0.25
A + EO	−3.73	5	8.88	1.06	0.19
Simpson (SIM)					
A + EO	−0.66	5	11.01	0.00	0.42
A + EO + T	−1.76	6	12.64	1.64	0.19
A + EO + BO	−1.46	6	12.94	1.93	0.16
Marin (MAR)					
Constant	34.34	2	39.20	0.00	0.52

[a] Model notation indicates structure for effects of owl age (A), even-odd years (EO), linear time (T), quadratic time (TT), or barred owls (BO).
[b] K = no. parameters in model, including covariance parameters.
[c] ΔAIC$_c$ = difference between the model listed and the best AIC$_c$ model.

a

Wenatchee ···· Cle Elum —·· Rainier --- Olympic

$\bar{x}$ fecundity vs Year (1985–2003)

b

Coast Ranges / HJ Andrews / Warm Springs / Tyee / Klamath / South Cascades

$\bar{x}$ fecundity vs Year (1985–2003)

c

NW California ···· Hoopa --- Simpson —·· Marin
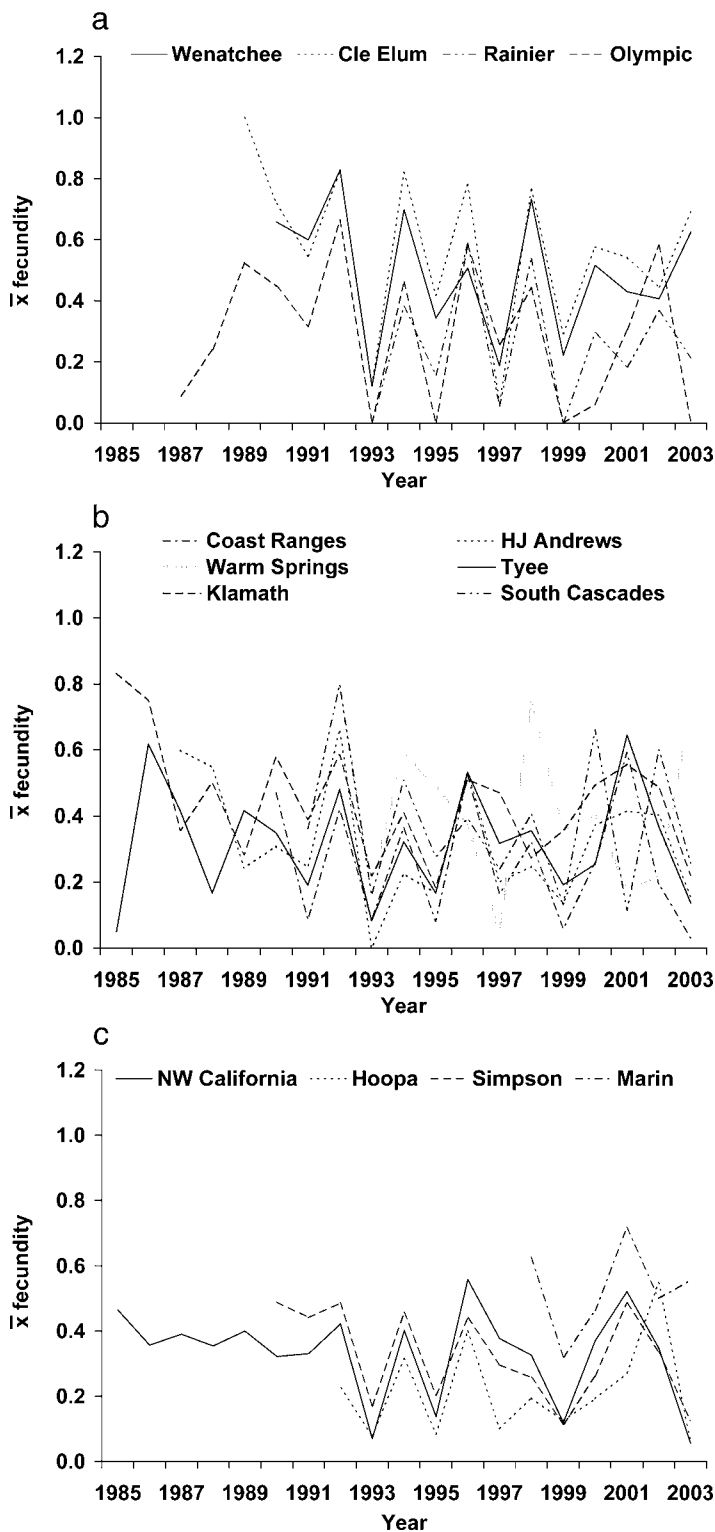
$\bar{x}$ fecundity vs Year (1985–2003)

Figure 2. Annual fluctuations of mean fecundity (no. young fledged per female) of northern spotted owls in 4 study areas in Washington (a), 6 study areas in Oregon (b), and 4 study areas in California (c).

Table 7. Regression coefficients ($\hat{\beta}$) from the best model containing linear (T) or quadratic (TT) time trends on the number of young fledged (NYF) by northern spotted owl in 14 study areas in Washington, Oregon, and California.

Study area[a]	Best time trend model[b]	ΔAIC_c[c]	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington						
WEN	A + EO + T	1.325	−0.022	0.017	−0.055	0.011
CLE	A + EO + T	0.305	−0.038	0.024	−0.085	0.009
RAI	A*EO + T	5.534	0.005	0.011	−0.016	0.026
OLY	A + EO + T	2.935	−0.005	0.013	−0.030	0.020
Oregon						
COA	A + EO + T	1.529	−0.014	0.011	−0.036	0.008
HJA	A + EO + TT[d]	0.000	−0.024	0.011	−0.046	0.002
			0.009	0.003	0.003	0.015
WSR	A + T	3.444	0.007	0.028	−0.048	0.062
TYE	A + T	0.000	0.016	0.008	0.000	0.317
KLA	A + T	2.384	0.004	0.009	−0.014	0.022
CAS	A + EO + T	0.000	−0.034	0.017	−0.067	0.001
California						
NWC	A + T	0.000	−0.019	0.010	−0.039	0.001
HUP	A + EO + T	0.000	0.023	0.011	0.001	0.044
SIM	A + EO + T	1.636	−0.010	0.009	−0.028	0.008
MAR	A + T	7.995	0.029	0.092	−0.151	0.209

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Oregon Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] Notation indicates model structure for effects of age (A), even-odd year (EO), linear time trend (T), or quadratic time trend (TT).
[c] ΔAIC_c = difference between the best time-trend model and the best AIC_c model for each study area (Appendix F).
[d] The first estimate is the linear term, and the second is the quadratic term.

discernable pattern of residual variance among study areas. Total variability ranged from 0.495 (HUP) to 0.969 (CLE), but again there was no discernable pattern to the magnitude of variability among study areas.

Meta-analysis of Fecundity.—The ranking of models in the meta-analysis of all 14 study areas and the 8 monitoring areas was nearly identical. There were differences between the 2 analyses only in the ordering of models with essentially no support (Akaike weights < 0.00); therefore, we present the results for only the 14 study areas combined. The best model included additive effects of region and a variable time effect (region + t); it contained 55% of the weight of evidence (Table 10). Time trends (T) in fecundity were not supported by the meta-analysis; the highest-ranking trend model was (region + T) with an AIC weight of 0.000. Models that included ownership (O) effects also were ranked much lower than the best model (AIC weight = 0.015). Estimates of adult female fecundity by region, averaged over years, indicated that fecundity was highest for the mixed-conifer region in Washington and lowest for the Douglas-fir region of Washington and the Oregon coast (Table 11). Fecundity was intermediate for the Douglas-fir region of the Oregon Cascades, the mixed-conifer region of California and Oregon, and the redwood region of coastal California.

The even-odd year (EO) effect was not as important in the meta-analysis as it was in the analyses of individual study areas,

areas in Oregon (Table 9). Three of the 4 study areas with the lowest (<10%) temporal variation were in California (NWC, SIM, and MAR). Residual variance was by far the greatest component of total variance (ranging from 68 to 92%) and was due largely to individual heterogeneity among owls. There was no

Table 8. Regression coefficients ($\hat{\beta}$) for the effect of barred owls on the number of young fledged (NYF) by northern spotted owls in 14 study areas in Washington, Oregon, and California. Estimates are from the best model with the barred owl (BO) covariate.

Study area[a]	Model[b]	ΔAIC_c[c]	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington						
WEN	A + EO + BO	1.173	−0.942	0.701	−2.316	0.433
CLE	A + EO + BO	2.533	−0.550	1.102	−2.710	1.610
RAI	A + EO + BO	10.700	0.202	0.548	−0.871	1.275
OLY	A + EO + BO	1.744	−1.026	0.872	−2.735	0.682
Oregon						
COA	A + EO + BO	1.907	−0.280	0.259	−0.787	0.228
HJA	A + EO + BO	9.604	−0.428	1.011	−2.411	1.554
WSR	A + BO	3.355	−0.503	1.316	−3.081	2.078
TYE	A + BO	1.915	0.733	0.580	−0.404	1.869
KLA	A + BO	1.875	1.316	1.617	−1.853	4.484
CAS	A + EO + BO	2.755	−1.385	1.270	−3.874	1.105
California						
NWC	A + BO	1.253	−2.069	1.278	−4.575	0.436
HUP	A + EO + BO	0.525	2.114	1.058	0.040	4.187
SIM	A + EO + BO	1.929	−1.932	2.144	−6.134	2.270
MAR	BO	1.102	22.533	15.951	8.730	53.797

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] Notation indicates model structure for effects of age (A), even-odd year (EO), or barred owls (BO).
[c] Δ_i = difference between the best model with the BO covariate and the best AIC$_c$ model for each study area (Appendix F).

but it was apparent between 1990 and 2000 (Fig. 3). The higher ranking of the year-specific model (region + t) was likely due to the additional power from the combined data to detect individual year effects. This model also detected the waning of the even-odd year effect in more recent years and the variability in amplitude of the difference between even and odd years. There appeared to be a downward trend in the yearly fluctuations of fecundity (Fig. 3), but we were not able to verify this in our analysis.

Although the model that included the BO covariate was the second best in both meta-analyses, this was attributed primarily to the region and even-odd year effects in the model. The estimate of the regression coefficient for the BO effect for this model (all areas combined) was −0.404 (SE = 0.340). Thus, the 95% confidence interval on this effect was large (−1.069 to 0.262) and overlapped 0.0 substantially. In general, models containing the BO covariate were not highly ranked for both meta-analyses on the number of young fledged.

Apparent Survival Rates

Individual Study Areas.—We used 4,963 banded nonjuvenile spotted owls to estimate apparent survival rates, including 574 1-year-old owls, 684 2-year-old owls, and 3,705 adults (Table 1). The number of recaptures of marked owls was approximately 5 times the number of initial markings, which resulted in 32,054 initial captures and recaptures. The overall χ^2 goodness of fit for the global model from Program RELEASE was 1600.03 with 925 degrees of freedom ($\hat{c}$ = 1.73, $P < 0.001$), indicating that there was good fit of the data to Cormack–Jolly–Seber open population models (Table 12). Estimates of $\hat{c}$ for the individual study areas ranged from 0.84 to 2.74 (Table 12), which indicated no to moderate overdispersion of recaptured owls and good fit of the data to the models. The lack of fit that occurred was due to no detection or temporary emigration of owls from study areas with subsequent returns in later years.

Annual estimates of recapture probabilities, p, were between 0.70 and 0.95 on most study areas (Appendix D). However, there were occasional years when $\hat{p} < 0.70$ on the WEN, RAI and OLY

Table 9. Variance components of the number of young fledged (NYF) by northern spotted owls from a mixed-model analysis of year- and territory-specific estimates. Spatial variability is the random effects estimate of territory variability, and temporal variability is the random effects estimate of year variability.

Study area[a]	Spatial Estimate	Spatial % of total	Temporal Estimate	Temporal % total	Residual Estimate	Residual % total	Total Estimate
Washington							
WEN	0.058	6	0.166	18	0.691	75	0.915
CLE	0.058	5	0.227	23	0.684	70	0.969
RAI	0.000	0	0.109	17	0.505	82	0.613
OLY	0.021	2	0.201	28	0.481	68	0.703
Oregon							
COA	0.015	2	0.127	21	0.450	76	0.592
HJA	0.000	0	0.108	15	0.601	84	0.709
WSR	0.000	0	0.195	22	0.675	77	0.871
TYE	0.030	4	0.079	11	0.569	83	0.678
KLA	0.000	0	0.056	7	0.704	92	0.760
CAS	0.022	2	0.153	19	0.615	77	0.790
California							
NWC	0.028	3	0.059	8	0.623	87	0.710
HUP	0.035	7	0.056	11	0.404	81	0.495
SIM	0.025	3	0.054	8	0.585	88	0.663
MAR	0.108	12	0.058	6	0.701	80	0.867

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Oregon Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.

Table 10. Model selection results from the meta-analysis of the number of young fledged by female northern spotted owls on 14 study areas in Washington, Oregon, and California.

Model[a]	−2log$\mathscr{L}$	K[b]	AIC$_c$	ΔAIC$_c$[c]	Akaike weight
region + t	57.215	26	117.238	0.000	0.547
region + t + BO	55.832	27	118.522	1.284	0.288
t	72.838	21	119.972	2.734	0.139
owner + t	72.182	23	124.385	7.147	0.015
region*BO + t	48.627	32	125.124	7.886	0.011
region + EO	141.543	9	160.480	43.242	0.000
region*EO	133.320	14	163.566	46.328	0.000
owner + EO	154.193	6	166.624	49.386	0.000
owner*EO	153.921	8	170.668	53.430	0.000
owner*t	47.154	54	195.562	78.324	0.000
region + T	190.340	9	209.277	92.039	0.000
region + BO	193.846	9	212.784	95.546	0.000
T	205.554	4	213.757	96.519	0.000
region*BO	188.671	13	216.607	99.369	0.000
owner + T	204.825	6	217.255	100.018	0.000
Constant	211.243	3	217.364	100.127	0.000
BO	210.334	4	218.537	101.299	0.000
region*T	188.294	14	218.540	101.302	0.000
owner*T	204.686	8	221.432	104.194	0.000

[a] Notation indicates model structure for effects of geographic region (region), landownership (owner), even-odd year (EO), annual time (t), linear time (T), or barred owls (BO).
[b] K = no. parameters in model, including covariance parameters.
[c] ΔAIC$_c$ = difference between the model listed and the best AIC$_c$ model.

study areas in Washington and the KLA study area in Oregon (Appendix D). The most unusual case was a year on the OLY study area for which $\hat{p} = 0.26$ following a winter with record snowfall and persistent snow on the ground during spring (Appendix D). Recapture probabilities were constant among years for 3 study areas (COA, NWC, SIM). The best model structure on recapture probabilities varied among study areas with 1 or more areas having effects of sex (s), productivity (r), presence of barred owls (BO), time (t), or time trends (T; Table 13). For 6 study areas, there was an increasing time trend (T or TT) in recapture probabilities in 1 or more of the competitive models (ΔQAIC$_c$ < 2.0), indicating that field biologists got better at locating and reobserving banded owls as the studies progressed.

The best model structure for apparent survival, φ, was not consistent among study areas (Table 13). Age, sex, presence of barred owls, time, or time trends were important effects on apparent survival in 1 or more of the best models. Age of owls was important on 8 of the 14 study areas (Table 13). On average,

Table 11. Estimates of mean annual fecundity (no. female young produced/per female) of adult northern spotted owls for 6 geographic regions.

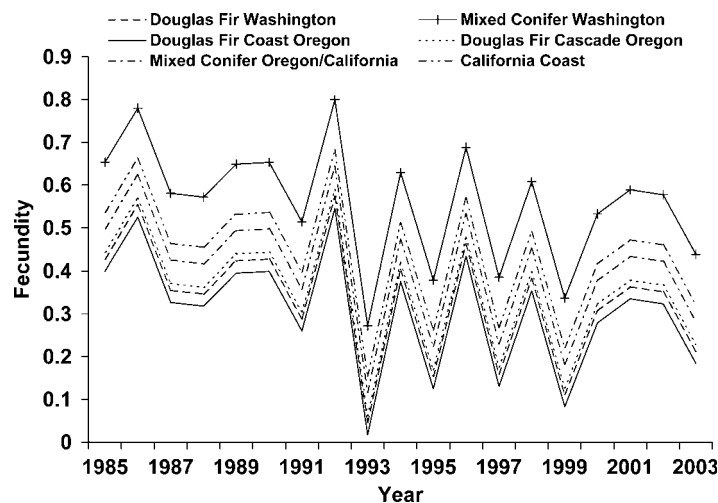| Geographic region	$\bar{x}$	SE	95% CI Lower	95% CI Upper
Washington—Douglas-fir	0.313	0.041	0.233	0.393
Washington—mixed-conifer	0.560	0.041	0.480	0.640
Oregon Coastal—Douglas-fir	0.306	0.039	0.230	0.382
Oregon Cascades—Douglas-fir	0.404	0.034	0.337	0.471
Oregon/California—mixed-conifer	0.350	0.032	0.287	0.413
California Coast	0.442	0.045	0.354	0.530

Figure 3. Annual fluctuations of mean fecundity (no. young fledged per female) of northern spotted owls in 6 geographic regions, based on the best model (region + time) from a meta-analysis of 14 study areas.

apparent survival was higher for older owls with rates ranging from 0.42 to 0.86 for 1-year-olds ($\bar{x} = 0.68$, SE = 0.054), 0.63 to 0.89 for 2-year-olds ($\bar{x} = 0.81$, SE = 0.030), and 0.75 to 0.92 for adults ($\bar{x} = 0.85$, SE = 0.016) (Table 13). Apparent survival rates for adults were >0.85 for most study areas except WEN, WSR, MAR, and RAI. Apparent survival rates were different between

Table 12. Estimates of overdispersion ($\hat{c}$) in capture–recapture data from 14 northern spotted owl demographic study areas in Washington, Oregon and California.

Study area[a]	CJS[b] χ^2	CJS[b] df	CJS[b] $\hat{c}$	λ_{RJS}[b] χ^2	λ_{RJS}[b] df	λ_{RJS}[b] $\hat{c}$
Washington						
WEN	165.67	71	2.33	147.42	84	1.18
CLE	63.92	68	0.94	35.21	51	0.69
RAI	45.24	46	0.98	33.73	47	0.72
OLY	170.35	86	1.98	156.42	104	1.50
Oregon						
COA	179.51	68	2.64	168.87	56	3.02
HJA	210.40	85	2.47	167.29	78	2.14
WSR	49.31	46	1.07	46.95	41	1.14
TYE	133.41	95	1.40	69.68	64	1.09
KLA	117.93	95	1.24	87.48	74	1.18
CAS	139.67	62	2.25	142.91	65	2.20
California						
NWC	86.84	75	1.16	124.93	81	1.54
HUP	41.07	49	0.84	46.06	52	0.89
SIM	186.39	68	2.74	139.81	50	2.80
MAR	10.33	11	0.94	NA[c]	NA[c]	NA[c]
Totals	1,600.04	925	1.73	1,366.76	847	1.61

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] CJS indicates data sets used for Cormack–Jolly–Seber estimates of apparent survival, and λ_{RJS} indicates data sets used to estimate annual rates of population change. Values for χ^2 and df are from tests 2 and 3 in Program RELEASE. Estimates of $\hat{c}$ <1.0 were set to 1.00 for analysis.
[c] λ_{RJS} could not be estimated for the MAR study area because of small sample size.

Table 13. Estimates of apparent survival rates ($\hat{\phi}$) for 3 age classes of northern spotted owls on 14 study areas in Washington, Oregon, and California.

Study area[a]	Best model[b] φ structure	p structure	1 year old[c] $\hat{\phi}$	SE($\hat{\phi}$)	2 years old[c] $\hat{\phi}$	SE($\hat{\phi}$)	≥3 years old[c] $\hat{\phi}$	SE($\hat{\phi}$)
Washington								
WEN	(S1 = S2, A) + BO	T	0.626	0.073	0.626	0.073	0.750	0.026
CLE	t	s + r	0.860	0.017	0.860	0.017	0.860	0.017
RAI	T	t	0.832	0.020	0.832	0.020	0.832	0.020
OLY	(S1, S2 = A) + BO	t	0.570	0.117	0.855	0.011	0.855	0.011
Oregon								
COA	S1, S2 = A	(.)	0.721	0.107	0.886	0.010	0.886	0.010
HJA	S1, S2 = A	TT	0.415	0.111	0.883	0.010	0.883	0.010
WSR	(.)	r + BO	0.823	0.015	0.823	0.015	0.823	0.015
TYE	(S1, S2 = A) + TT	s + T	0.817	0.042	0.878	0.011	0.878	0.011
KLA	(.)	T	0.849	0.009	0.849	0.009	0.849	0.009
CAS	S1 = S2, A	TT	0.725	0.079	0.725	0.079	0.854	0.014
California								
NWC	(S1 = S2, A) + TT	meth + by	0.810	0.027	0.810	0.027	0.869	0.011
HUP	S1 = S2, A	TT*EW	0.781	0.049	0.781	0.049	0.853	0.014
SIM	(.)	s	0.850	0.010	0.850	0.010	0.850	0.010
MAR	s	s + r ♀	0.824	0.045	0.824	0.045	0.824	0.045
		s + r ♂	0.913	0.035	0.913	0.035	0.913	0.035

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.

[b] Model notation indicates structure for additive (+) or interactive (*) effects of sex (s), time (t), linear time trend (T), quadratic time trend (TT), reproduction (r), barred owls (BO), age class (S1, S2, A), east–west binomial subdivision of study area (EW), survey method (meth), or years of poor weather (by). For age-classes, an (=) sign means that age classes were combined, and a (,) indicates that they were modeled separately. Age classes (S1, S2, A) indicate owls that were 1, 2, or 3 years old.

[c] For study areas with time structure in the top model, we estimated average survival as follows: for variable time (t) models, we calculated the arithmetic mean and standard error using the delta method. For linear (T) models, we used the median value and its standard error (odd no. survival estimates) or the lower of the 2 median values and its standard error (even no. survival estimates). For quadratic (TT) models, we used the annual estimate from the model that was closest to the arithmetic average of the maximum and minimum annual survival estimates.

males and females for only the MAR study area, and the effect of barred owls was important only for the WEN and OLY study areas (also see below).

The best or competitive ($\Delta QAIC_c$ < 2.0) models for apparent survival suggested a linear or quadratic time effect for 11 of the 14 study areas (Table 14). There was strong evidence for declines in apparent survival on 5 study areas (WEN, CLE, RAI, OLY, NWC; Table 14, Fig. 4). In addition, there was evidence for a slight decrease in apparent survival on COA during the last 5 years of study (Table 14; Fig. 4b). Declines in apparent survival were most evident in Washington (Fig. 4a), where all β estimates were negative and 95% confidence intervals for 3 (WEN, RAI, OLY) of the 4 study areas did not overlap zero. In addition, apparent survival for owls on the WEN and RAI areas during the latter years of the study were <0.80, which were the lowest rates recorded for the 14 study areas. In Oregon, there were no time trends in apparent survival rates for 4 (HJA, KLA, WSR, CAS) of the 6 study areas (Table 14; Fig. 4b). Apparent survival rates for COA increased slightly during the early years of the study, then decreased slightly from 1997 to 2003. In contrast, apparent survival rates on the TYE study area decreased during the initial years of the study, then increased from 1995 to 2003. In California, there was a significant linear decline in apparent survival on the NWC study area (Fig. 4c) and evidence of a slight decline on the SIM area. There was little evidence of time trends in apparent survival on the HUP and MAR study areas.

Meta-analysis of Adult Apparent Survival.—We used 5,342 and 3,702 encounter histories (initial captures + recaptures) in the meta-analysis of apparent survival for all 14 study areas and the 8 monitoring areas, respectively. Estimates of $\hat{c}$ from Program RELEASE were 1.730 for the 14 study areas combined and 1.738 for the 8 monitoring areas (Table 12), indicating good fit of the data to Cormack–Jolly–Seber open population models. Because results for all 14 study areas and the 8 monitoring areas were similar, we only report results for all study areas.

The best model for the meta-analysis of the 14 study areas was {φ(region + t) p(g + t + s)} with 55 parameters. This model indicated both regional and variable time effects on apparent survival with study area, time, and sex effects on recapture probabilities (Table 15). This model accounted for 78% of the weight of evidence (Akaike weight) among all the models, so it was strongly supported by the data. There was no evidence of a sex effect on survival as noted by the differences in $QAIC_c$ for models {φ(g + t) p(g + s + t)} and {φ(g + t + s) p(g + s + t)} (Table 15). The highest-ranked model with a sex effect on φ was {φ(g + t + s) p(g + t + s)} with 64 parameters; this model had a $\Delta QAIC_c$ of 6.45 and an Akaike weight of only 0.031. Similarly, there was little evidence of latitude or ownership effects in the meta-analysis of survival; $\Delta QAIC_c$ values for models φ(latitude + t) and φ(ownership + t) were >12.00, suggesting that latitude and ownership were not good surrogates for the study area effect in the highest-ranked model. Because of the high Akaike weight of the top model, it was used to estimate apparent survival of adults (Fig. 5). There was variation in survival rates among regions and

Table 14. Beta estimates (β̂) for the best models that included a time trend on apparent survival of nonjuvenile northern spotted owls on 14 study areas in Washington, Oregon, and California.

Study area[a]	Model trend[b]	$\Delta QAIC_c$[c]	β̂	SE	CV[d]	95% CI Lower	95% CI Upper
Washington							
WEN	TT[e]	0.341	−0.078	0.029	0.372	−0.138	−0.021
			−0.020	0.009	0.450	−0.038	−0.002
CLE	T	2.063	−0.030	0.024	0.800	−0.076	0.016
RAI	T	0.000	−0.275	0.069	0.251	−0.409	−0.140
OLY	T	1.253	−0.049	0.025	0.510	−0.097	−0.001
Oregon							
COA	TT[e]	0.282	0.016	0.027	1.688	−0.037	0.069
			−0.016	0.009	0.563	−0.033	0.000
HJA	T	1.122	−0.022	0.023	1.045	−0.067	0.023
WSR	(S1, S2 = A)*T[f]	0.607	−0.012	0.039	3.250	−0.088	0.064
			1.545	0.941	0.609	−0.299	3.389
TYE	TT[e]	0.000	−0.003	0.021	7.000	−0.043	0.038
			0.008	0.004	0.500	0.000	0.015
KLA	T	1.973	0.005	0.017	3.400	−0.029	0.038
CAS	T	2.010	0.003	0.032	10.667	−0.059	0.066
California							
NWC	TT[e]	0.000	−0.031	0.015	0.484	−0.060	−0.003
			0.003	0.003	1.000	−0.003	0.009
HUP	TT[e]	0.441	0.002	0.038	19.000	−0.072	0.077
			0.025	0.014	0.560	−0.002	0.051
SIM	T	1.596	−0.015	0.024	1.600	−0.062	0.032
MAR	T	2.118	0.048	0.206	4.292	−0.357	0.452

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] T = linear trend over time, TT = quadratic trend over time.
[c] $\Delta QAIC_c$ = difference between the model listed and the best $QAIC_c$ model.
[d] Coefficient of sampling variation (CV) computed as SE ($\hat{\beta}_i / |\hat{\beta}_i|$).
[e] The first row estimate is the linear term, and the second is the quadratic term.
[f] First row is for linear term, second is for interaction.

years with the highest apparent survival for the Douglas-fir region of the Oregon coast and lowest for the mixed-conifer region of eastern Washington, which was opposite of the regional differences for fecundity. Results also suggested a downward trend in survival with time (Fig. 5); however, the year-to-year variation was so large that time trend models did not rank high in the list of models (Table 15). As a result, we fit 2 a posteriori models {ϕ(region*T) p(g + t + s)} and {ϕ(region + T) p(g + t + s)} to the data to test for a time trend in apparent survival. Because model {ϕ(region*T) p(g + t + s)} with 44 parameters was the more highly ranked of these 2 models (Table 15), we investigated the interaction between region and time trends (Fig. 6). This relation indicated that the major downward trends in survival were taking place in the mixed-conifer and Douglas-fir regions of Washington. This result was consistent with the results of individual study areas where we found declines in apparent survival rates for the study areas in Washington.

Correlation Between Reproduction and Survival.—The $\Delta QAIC_c$ for the highest-ranked model that included the reproductive effect (r) was 18.40, suggesting that reproduction had little effect on survival; however, this value applies to differences among models and not necessarily the importance of individual variables in the model. Consequently, we examined the estimates of the individual variable effects, β estimates, and their confidence intervals in the best model where the r effect occurred,

model {ϕ(region + r) p(g + t + s)} (Table 15). Results from this analysis indicated a negative relation between NYF in a given year and survival the following year. The β estimate of the r coefficient for this model was −0.257 (95% confidence interval = −0.432 to −0.082). Similarly, the estimate of β for the r coefficient for the same model for the 8 monitoring areas was −0.292 (95% confidence interval = −0.507 to −0.078). These results indicated that high reproduction in a year was followed by lower survival rates the following year, but this effect was found in just a few regions as shown by model {ϕ(region*r) p(g + t + s)}. The strength of this relationship was greatest in the more northern latitudes and higher-elevation study areas, particularly the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir zone of the Oregon Cascades (Table 16). This effect, if any, was small for study areas in California and the mixed-conifer and coastal Douglas-fir regions in Oregon.

Effects of Landownership.—Model {ϕ(ownership + t) p(g + t + s)} with 52 parameters had a $\Delta QAIC_c$ of 13.43, and the 95% confidence intervals for the estimate for this effect included 0.0 (Table 15). Similarly, the model with landownership in the meta-analysis on the 8 monitoring areas {ϕ(ownership + t) p(g + t + s)} had 45 parameters and a $\Delta QAIC_c$ of 11.55, and the 95% confidence interval for this effect included 0.0. Thus, there was little evidence that landownership was an important predictor of apparent survival rates.
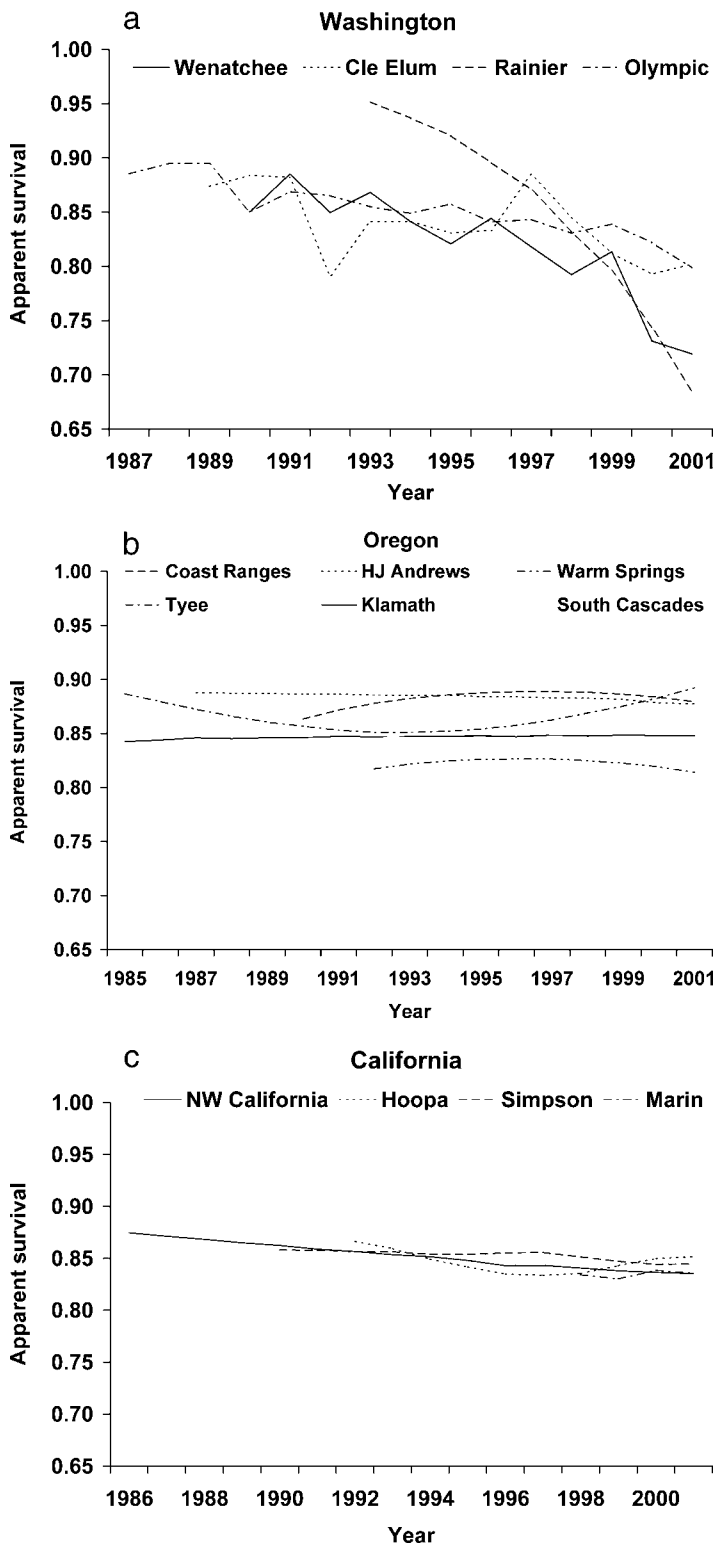
Figure 4. Model averaged estimates of apparent survival of territorial female northern spotted owls in 4 study areas in Washington (a), 6 study areas in Oregon (b), and 4 study areas in California (c).
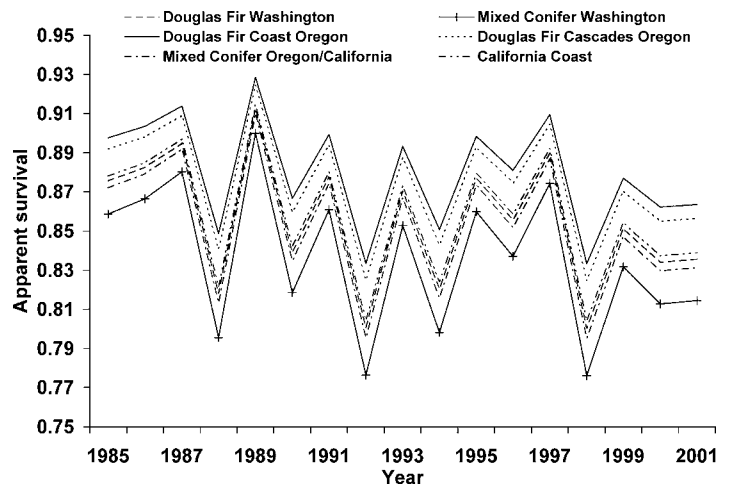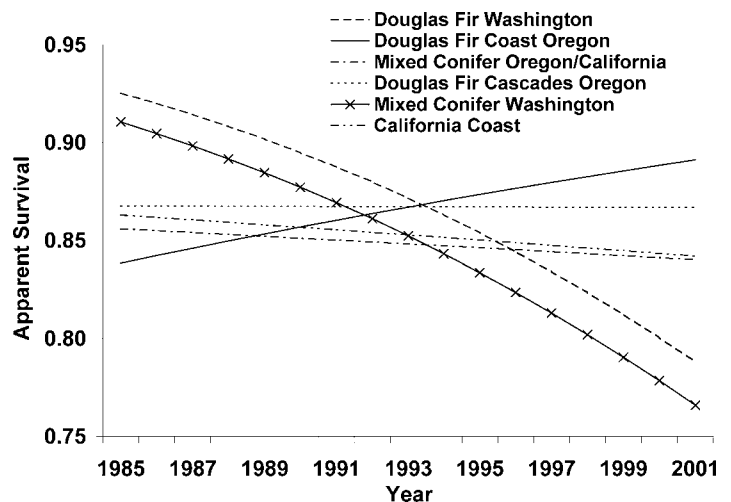

Figure 5. Estimates of apparent survival rates of adult female northern spotted owls in 6 geographic regions from the meta-analysis of 14 study areas and based on model $\{\phi \text{ (region} + t) \, p(g + t + s)\}$.

Effects of Barred Owls in Analyses of Individual Study Areas.—In the analysis of the 14 study areas, we found a negative effect of barred owls ($\hat{\beta} = -6.75$, 95% CI $= -11.65$ to -1.86) on recapture probabilities (p) of spotted owls for only the WSR study area. The effects of barred owls on recapture probabilities was positive for some areas, opposite to what we hypothesized. In contrast, we found strong evidence for a negative effect of barred owls on apparent survival in the OLY and WEN study areas (Tables 13, 17); estimates of β and 95% confidence intervals for the 2 areas were -4.24 (-7.83 to -0.65) and -4.69 (-7.32 to -2.07), respectively. There also was some evidence for a negative effect of barred owls on apparent survival in the CLE, HJA, and NWC study areas, as models with the barred owl effect were competitive with the top models. Results for the RAI study area suggested that barred owls had a positive effect on spotted owl survival, but we believe this result was spurious. The best model of survival for RAI, $\phi(T)$, was 10.86 ΔAICs better than $\phi(BO)$. In

Figure 6. Estimates of apparent survival rates of adult female northern spotted owls in 6 geographic regions from the meta-analysis of 14 study areas based on model $\{\phi(\text{region*T}) \, p(g + t + s)\}$.

Table 15. Model selection criteria for models used in the meta-analysis of apparent survival of adult northern spotted owls on 14 demographic study areas in Washington, Oregon, and California, 1985–2003.

Model[a]	$QAIC_c$	$\Delta QAIC_c$[b]	Akaike weights	K[c]	Q deviance[d]
ϕ(region + t) p(g + s + t)	18,459.906	0.000	0.780	55	7,206.936
ϕ([owner*region] + t) p(g + s + t)	18,464.024	4.119	0.099	58	7,205.020
ϕ(g + t) p(g + s + t)	18,464.554	4.648	0.076	63	7,195.489
ϕ(g + s + t) p(g + s + t)	18,466.353	6.448	0.031	64	7,195.277
ϕ(region*T) p(g + s + t)	18,468.722	8.816	0.010	44	7,237.861
ϕ(latitude + t) p(g + s + t)	18,472.213	12.307	0.002	51	7,227.286
ϕ(s + t) p(g + s + t)	18,473.263	13.357	0.001	51	7,228.335
ϕ(owner + t) p(g + s + t)	18,473.338	13.433	0.001	52	7,226.400
ϕ(region*r) p(g + s + t)	18,478.302	18.396	0.000	44	7,247.441
ϕ(region + r) p(g + s + t)	18,478.557	18.652	0.000	39	7,257.737
ϕ(g + t) p(g + t)	18,479.624	19.719	0.000	62	7,212.572
ϕ(g + s + t) p(g + t)	18,480.976	21.070	0.000	63	7,211.912
ϕ([g*BO]+s) p(g + s + t)	18,483.279	23.374	0.000	61	7,218.240
ϕ([g*T] + s) p(g + s + t)	18,483.811	23.905	0.000	61	7,218.771
ϕ(region + T) p(g + s + t)	18,484.238	24.332	0.000	39	7,263.419
ϕ([g*TT] + s) p(g + s + t)	18,489.309	29.403	0.000	75	7,196.079
ϕ(g + s + T) p(g + s + t)	18,491.662	31.756	0.000	48	7,252.764
ϕ(g + s) p(g + s + t)	18,492.032	31.126	0.000	47	7,255.143
ϕ(g + BO + s) p(g + s + t)	18,492.843	32.937	0.000	48	7,253.945
ϕ(g + s + TT) p(g + s + t)	18,493.620	33.715	0.000	49	7,252.713
ϕ(s) p(g + s + t)	18,502.671	42.765	0.000	34	7,291.888
ϕ(s + T) p(g + s + t)	18,502.852	42.946	0.000	35	7,290.062
ϕ(BO + s) p(g + s + t)	18,503.635	43.729	0.000	35	7,290.845
ϕ(s + TT) p(g + s + t)	18,504.377	44.471	0.000	36	7,289.581
ϕ([g*t] + s) p(g + s + t)	18,601.916	142.010	0.000	223	7,008.269
ϕ([g*t] + s) p(g + t)	18,616.032	156.126	0.000	222	7,024.429
ϕ([g*t] + s) p([g + t]*s)	18,627.672	167.767	0.000	251	6,976.690
ϕ([g*t] + s) p(r + s)	18,810.165	350.259	0.000	191	7,281.848
ϕ([g*t] + s) p(r*s)	18,812.197	352.291	0.000	192	7,281.841
ϕ([g*t] + s) p(r)	18,822.324	362.418	0.000	190	7,296.045
ϕ(g*t) p(g*s*t)	18,929.102	469.196	0.000	553	6,649.370
ϕ(g*s*t) p(g*s*t)	19,215.200	755.295	0.000	728	6,562.237

[a] Codes indicate model structure for additive (+) or interactive (*) effects of region (region), study area (g), sex (s), annual time (t), linear time trend (T), quadratic time trend (TT), landownership (owner), latitude (latitude), barred owls (BO), or reproduction (r).
[b] $\Delta QAIC_c$ = difference between the model listed and the best $QAIC_c$ model.
[c] No. parameters in model.
[d] Q deviance is the difference between $-2\log(\mathscr{L})/\hat{c}$ of the current model and $-2\log(\mathscr{L})/\hat{c}$ of the saturated model.

addition, the barred owl covariate for this area was a quadratic function (Appendix B), a much different trend than that for the other study areas. The evidence for the effects of barred owls on survival of spotted owls on the remaining study areas was weak ($2.0 < \Delta QAIC_c < 3.0$) to negligible ($\Delta QAIC > 3.0$).

Effects of Barred Owls in the Meta-analysis of Survival.— The barred owl covariate was not a good predictor of time variation in apparent survival in the meta-analysis of the 14 study areas. The $\Delta QAIC_c$ value for the best model containing barred owls $\{\phi(g*BO + s)\ p(g + t + s)\}$ for this analysis was 23.37 (Table 15). This analysis suggested that the effects of barred owls differed by study area with 9 negative and 5 positive estimates of β (Table 18). There was strong evidence of a negative effect of barred owls on apparent survival for WEN and OLY and some evidence of a negative effect for CLE. In contrast, there was evidence of a positive effect of barred owls on apparent survival for CAS, the opposite of our original hypothesis. This may be a spurious result as barred owls were detected at <10% of spotted owl territories on the CAS study area during our study (Appendix B). Confidence intervals for the effect of barred owls (β) broadly overlapped zero for the remainder of the study areas indicating little evidence of an effect. Study areas in California had the

lowest occurrence of barred owls at spotted owl territories (<5%), so the potential effect of barred owls on these study areas was minimal compared to study areas farther north, where barred owls were detected on many spotted owl territories (Appendix B).

Annual Rate of Population Change (λ)

Individual Study Areas.—We used 4,963 banded owls to estimate annual rates of population change (λ_{RJS}). Estimates of overdispersion (c) in the capture–recapture data ranged from 0.690 to 3.02 (Table 12) indicating reasonable fit of the data to the Cormack–Jolly–Seber models for most data sets. Estimates of λ could not be computed for the MAR study area because there were too few years of capture–recapture data for that area.

The sex- and time-specific model $\{\phi(s*t)\ p(s*t)\ \lambda(s*t)\}$ was not important for any of the study areas; therefore, we used the time-specific model $\{\phi(t)\ p(t)\ \lambda(t)\}$ for estimating temporal process variation (Table 19). Estimates of λ_{RJS} ranged from 0.896 to 1.005 for the 13 areas, and all but 1 (TYE) of the estimates were <1.0, suggesting population declines for most areas. There was strong evidence that populations on the WEN, CLE, WSR, and SIM study areas declined during the study (Table 19; Fig. 7), and there also was evidence that populations on the RAI, OLY, COA, and

Table 16. Estimates of $\hat{\beta}$ for the effect of reproduction (r) on apparent survival of adult northern spotted owls in 6 geographic regions. Estimates are from model $\{\phi(\text{region}*r)\ p(g+t+s)\}$ in the meta-analysis of 14 demographic study areas in Washington, Oregon, and California.

Region	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington Douglas-fir	−0.596	0.234	−1.055	−0.136
Washington mixed-conifer	−0.315	0.185	−0.677	0.047
Oregon Coastal Douglas-fir	−0.119	0.209	−0.530	0.291
Oregon Cascades Douglas-fir	−0.507	0.182	−0.863	−0.151
Oregon/California mixed-conifer	0.010	0.221	−0.424	0.443
California Coast	0.398	0.318	−0.226	1.023

HJA study areas were decreasing. Precision of the λ_{RJS} estimates for RAI and OLY were not sufficient to detect a significant difference from $\lambda = 1.00$. Moreover, the estimate of λ_{RJS} for RAI (0.896) was the lowest of all of the areas. Populations on TYE, KLA, CAS, NWC, and HUP appeared to be stationary during the study, but there was some suggestion that the last 3 were declining ($\hat{\lambda}_{\text{RJS}} < 1.00$) also. The weighted mean $\hat{\lambda}_{\text{RJS}}$ for all of the study areas was 0.963 (SE = 0.009, 95% CI = 0.945–0.981) which suggested a 3.7% decline per year over the period of study.

Of the 8 monitoring areas, there was evidence that populations were declining on CLE, OLY, COA and HJA based on 95% confidence intervals that did not overlap 1.0 or barely included 1.0. The remainder of the areas had confidence intervals that substantially overlapped 1.00, so we could not conclude that those populations were declining. The weighted mean $\hat{\lambda}_{\text{RJS}}$ for the 8

Table 17. Estimates of $\Delta QAIC_c$ and $\hat{\beta}$ for the effects of barred owls on apparent annual survival of adult northern spotted owls on 14 demographic study areas in Washington, Oregon, and California. Estimates were based on the best QAIC model that included the barred owl effect.

Study area[a]	$\Delta QAIC_c$[b]	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington					
WEN	0.00	−4.69	1.34	−7.32	−2.07
CLE	1.58	−1.40	0.99	−3.33	0.54
RAI	10.86	4.44	2.18	0.16	8.72
OLY	0.00	−4.24	1.83	−7.83	−0.65
Oregon					
COA	2.01	0.03	0.68	−1.31	1.37
HJA	0.89	−1.83	1.69	−5.14	1.48
WSR	2.04	0.08	1.57	−2.98	3.15
TYE	2.37	1.35	1.21	−1.03	3.72
KLA	2.05	0.02	3.34	−6.51	6.56
CAS	1.55	1.80	2.70	−3.49	7.10
California					
NWC	0.95	−2.39	1.68	−5.68	0.90
HUP	1.18	−3.18	3.10	−9.26	2.90
SIM	0.70	−5.80	5.05	−15.68	4.08
MAR	1.99	11.61	27.48	−42.26	65.48

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] $\Delta QAIC_c$ = difference between the best $QAIC_c$ model and the best model with the barred owl effect.

Table 18. Estimates of $\hat{\beta}$ for the effect of barred owls (B) on apparent survival of adult northern spotted owls from the meta-analysis of 14 study areas in Washington, Oregon, and California. Model was $\{\phi(\text{BO}*\text{region})\ p(g+s+t)\}$.

Study area[a]	$\hat{\beta}$	SE	95% CI Lower	95% CI Upper
Washington				
WEN	−4.122	1.218	−6.509	−1.734
CLE	−1.884	1.422	−4.671	0.904
RAI	2.241	2.209	−2.089	6.571
OLY	−4.718	1.649	−7.951	−1.485
Oregon				
COA	0.308	0.584	−0.836	1.452
HJA	−0.777	1.894	−4.889	2.936
WSR	−1.141	2.077	−5.211	2.929
TYE	2.544	1.523	−0.441	5.529
KLA	1.775	3.770	−5.614	9.165
CAS	6.813	2.804	1.317	12.309
California				
NWC	−2.256	2.087	−6.347	1.836
HUP	−3.678	4.398	−12.298	4.943
SIM	−4.919	4.245	−13.238	3.401
MAR	−5.702	47.727	−99.247	87.843

[a] Study area acronyms same as in Table 17.

monitoring areas was 0.976 (SE = 0.007, 95% CI = 0.962–0.990), which suggested an overall decline of 2.4% per year. The weighted mean $\hat{\lambda}_{\text{RJS}}$ for the other 6 study areas was 0.942 (SE = 0.016, 95% CI = 0.910–0.974), suggesting a decline of 5.8% per year.

Precision and Variance Components.—Precision of the estimates was good for most study areas; coefficients of variation ranged from 1.2 to 6.1% with a mean of 2.6% (Table 19). Precision of the estimates for RAI, OLY, CAS, and KLA was lower than those for the other areas, which resulted in wider confidence intervals and lower power to detect a difference in λ from 1.0. Precision of estimates was generally higher for density study areas than for territory-specific study areas, possibly because 2 of the density study areas (TYE, NWC) were the longest studies in the sample. Results of the variance components analysis provided little evidence of temporal variability for the CLE, COA, HJA, WSR, NWC, and HUP study areas (Table 19). Estimated temporal variability was highest for the OLY, CAS, and TYE study areas, but all confidence intervals included zero.

Meta-analysis of Annual Rate of Population Change.—The estimate of overdispersion (c) for the meta-analysis on the 4 DSAs was 1.54, indicating a good fit to the Cormack–Jolly–Seber model and, hence, to the Pradel (1996) model. The model with the lowest QAIC for this analysis was $\{\phi(g*t)\ p(g*t)\ \lambda(.)\}$ with 113 parameters, which indicated that λ_t did not differ among the 4 study areas or over time (Table 20). This model had 37% of the weight of evidence, but there were 3 other models that ranked high: $\{\phi(g*t)\ p(g*t)\ \lambda(\text{region})\}$, $\{\phi(g*t)\ p(g*t)\ \lambda(\text{ownership})\}$, and $\{\phi(g*t)\ p(g*t)\ \lambda(g)\}$. Neither the more general model $\{\phi(g*t)\ p(g*t)\ \lambda(g*t)\}$ with full time by study area interaction nor the model $\{\phi(g*t)\ p(g*t)\ \lambda(g+t)\}$ with parallel changes in λ_t among study areas over time received any support. The weighted mean

Table 19. Estimates of $\hat{\lambda}_{RJS}$ and temporal process standard deviation ($\hat{\sigma}_{temporal}$) for northern spotted owls on 13 study areas in Washington, Oregon, and California. Estimates are based on mean (intercepts only) random effects models using time-specific estimates of ϕ, p and λ, except where noted.

Area[a]	Model[b]	$\hat{\lambda}_{RJS}$	SE	CV	95% CI Lower	95% CI Upper	$\hat{\sigma}_{temporal}$	95% CI Lower	95% CI Upper
Density study areas									
TYE	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	1.005	0.019	0.019	0.967	1.043	0.050	0.000	0.126
NWC	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.985	0.013	0.013	0.959	1.011	0.000	0.000	0.017
HUP	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.980	0.019	0.019	0.943	1.017	0.000	0.000	0.131
SIM	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.970	0.012	0.012	0.947	0.993	0.015	0.000	0.077
Territory study areas[c]									
WEN	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.917	0.018	0.019	0.882	0.952	0.038	0.000	0.147
CLE	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.938	0.019	0.020	0.901	0.976	0.000	0.000	0.090
RAI	$\phi(t)\ p(t)\ \gamma(t)$[d]	0.896	0.055	0.061	0.788	1.003	[d]	[d]	[d]
OLY	$\phi(ea^*t)\ p(ea^*t)\ \lambda(ea^*t)\ RE\lambda(mean)$	0.956	0.032	0.034	0.893	1.018	0.091	0.000	0.222
COA	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.968	0.018	0.019	0.932	1.004	0.000	0.000	0.067
HJA	$\phi(ea^*t)\ p(ea^*t)\ \lambda(ea^*t)\ RE\lambda(mean)$	0.978	0.014	0.015	0.950	1.005	0.000	0.000	0.064
WSR	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(mean)$	0.908	0.022	0.024	0.866	0.951	0.000	0.000	0.152
KLA	$\phi(t)\ p(t)\ \lambda(t)\ RE\lambda(T)$	0.997	0.034	0.042	0.930	1.063	0.026	0.000	0.135
CAS	$\phi(ea^*t)\ p(ea^*t)\ \lambda(ea^*t)\ RE\lambda(mean)$	0.974	0.035	0.035	0.906	1.042	0.082	0.000	0.269
Weighted mean for density study areas		0.982	0.007						
Weighted mean for territory study areas		0.963	0.010						
Weighted mean for all areas		0.963	0.009						

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] Best capture–recapture model structure from analysis of the a priori model set. Model notation indicates structure for effects of time (t), expansion year (ea), linear time trend (T), or constant (mean). RE = random effects.
[c] Marin Study Area not included because sample was too small to estimate λ.
[d] Model fit using a ϕ and γ parameterization; λ was calculated via arithmetic mean.

estimate of λ_{RJS} from the best model was 0.982 (SE = 0.007) with a 95% confidence interval of 0.968–0.996.

The results from model $\{\phi(g^*t)\ p(g^*t)\ \lambda(g)\}$ indicated that there were slight differences among the 4 study areas and time effects (Fig. 7). The λ_t associated with the different geographic regions from model $\{\phi(g^*t)\ p(g^*t)\ \lambda(region)\}$ indicated slightly higher λ_t for the Douglas-fir region on the Oregon coast (TYE), lower λ_t for the mixed-conifer region of California (NWC, HUP), and lowest λ_t for the redwood region of the California coast (SIM). The λ_t associated with different ownership categories from model
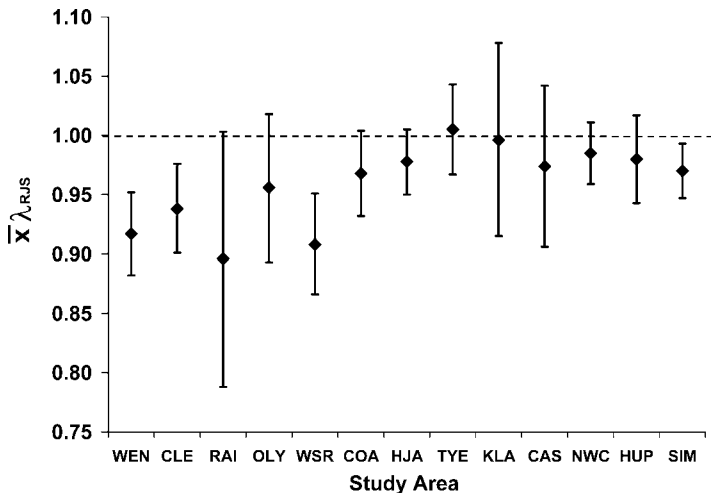

Figure 7. Estimates of mean annual rate of population change, λ_{RJS}, with 95% confidence intervals for northern spotted owls in 13 study areas in Washington, Oregon, and California based on random effects modeling and with model $\{\phi(t)\ p(t)\ \lambda(t)\}$, where t represents annual time changes.

$\{\phi(g^*t)\ p(g^*t)\ \lambda(ownership)\}$ indicated slightly higher $\hat{\lambda}$ for mixed ownership lands (TYE), followed by federal (NWC), then by private (HUP, SIM) lands. Confidence intervals for these estimates of λ overlapped substantially, and the $\hat{\lambda}_{RJS}$ for NWC and HUP were similar.

The estimate of overdispersion for the meta-analysis of the 9 TSAs was 1.62, indicating a good fit to the Cormack–Jolly–Seber model and, hence, the Pradel (1996) model. The model with the lowest QAIC was $\{\phi(g^*t)\ p(g^*t)\ \lambda(g^*t)\}$, which indicated that the annual rate of population change varied among study areas and years and that the change over time was different among study areas (i.e., a strong interaction among time and areas; Table 20). This model accounted for 100% of the model weight and was a much better fit to the data than the next best model $\{\phi(g^*t)\ p(g^*t)\ \lambda(ownership + t)\}$. As noted in the Methods, this analysis was hampered by numerical problems in fitting models to this large and complicated data set that included different starting and ending times and expansion areas in some studies. Among the small set of models that could be fit to the data, the most general model was the only one that received support. Grouping the study areas by ownership or region did not produce models that received any support (Table 20). This limited meta-analysis thus provided little reason to combine the area-specific analyses and suggested that inferences about population change should be based on individual study areas. A plot of the annual rates of population change for these areas from model $\{\phi(t)\ p(t)\ \lambda(t)\}$ clearly shows that changes in λ_t over time were quite different among study areas (Fig. 8).

Estimates of Realized Population Change.—Estimates of realized population change were based solely on the estimates of λ_t and represented the trend in numbers over the entire period

Table 20. Models selected in the meta-analysis of λ_{RJS} of northern spotted owls in Washington, Oregon, and California. Analyses were conducted separately for the 4 density study areas (1985–2003) and 10 territory study areas (1987–2003).

Model[a]	QAIC$_c$	ΔQAIC$_c$[b]	Akaike weight	K[c]
Density study areas				
ϕ(g*t) p(g*t) λ(.)	9,302.567	0.000	0.374	113
ϕ(g*t) p(g*t) λ(region)	9,303.128	0.561	0.283	115
ϕ(g*t) p(g*t) λ(owner)	9,303.418	0.851	0.244	115
ϕ(g*t) p(g*t) λ(g)	9,305.241	2.674	0.098	116
ϕ(g*t) p(g*t) λ(region + t)	9,316.061	13.494	0.000	129
ϕ(g*t) p(g*t) λ(owner + t)	9,316.800	14.233	0.000	129
ϕ(g*t) p(g*t) λ(g + t)	9,318.121	15.554	0.000	130
ϕ(g*t) p(g*t) λ(t)	9,318.896	16.329	0.000	127
ϕ(g*t) p(g*t) λ(region*t)	9,340.882	38.315	0.000	144
ϕ(g*t) p(g*t) λ(owner*t)	9,341.759	39.192	0.000	145
ϕ(g*t) p(g*t) λ(g*t)	9,354.079	51.512	0.000	152
Territory study areas				
ϕ(g*t) p(g*t) λ(g*t)	19,790.239	0.000	1.000	324
ϕ(owner*t) p(owner*t) λ(owner + t)	19,956.233	165.994	0.000	114
ϕ(owner*t) p(owner*t) λ(owner*t)	19,971.521	181.282	0.000	126
ϕ(t) p(t) λ(t)	19,981.221	190.982	0.000	69
ϕ(region*t) p(region*t) λ(region + t)	20,090.581	300.342	0.000	226

[a] Model notation indicates structure for study area (g), time (t), geographic region (region), landownership (owner), or constant (.).
[b] ΔQAIC$_c$ = the difference between the model listed and the best QAIC$_c$ model.
[c] No. parameters in model.
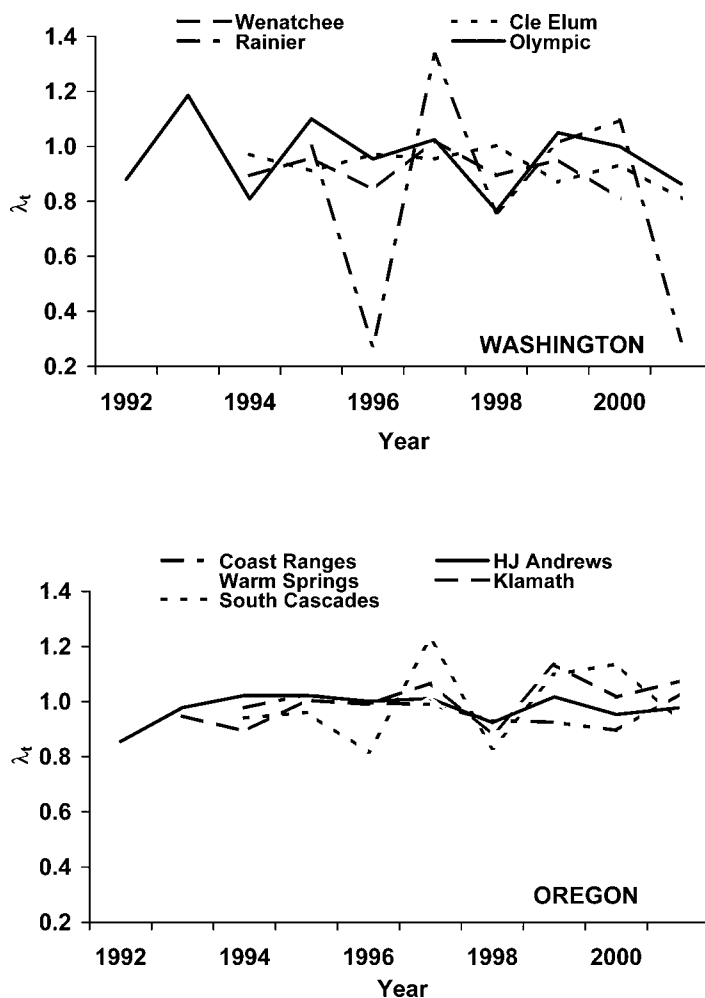
Figure 8. Estimates of annual rate of population change, λ_t, for northern spotted owls in 9 Territory Study Areas in Washington and Oregon from model {ϕ(t) p(t) λ(t)}, where t represents annual time changes.

of study for each of the 13 areas (Fig. 9). These trends represent the ratio of the population size in each focal year, expressed relative to the population in the first year. For example, if there were 100 owls on the CLE study area in 1994 and 54 in 2002, then the population in 2002 would be only 54% of the 1994 population. Based on this interpretation, there was strong evidence that populations on the CLE, WEN, OLY, RAI, WSR, HJA, COA, and SIM study areas declined during the study (Fig. 9a–c). Estimated population declines on the CLE, WEN, RAI, and WSR study areas were substantial over the past decade where population sizes were only 50–70% (30–50% decline) of the initial populations. Declines on the OLY, HJA, COA, and SIM study areas were not as great but are noteworthy; population sizes in 2002 were approximately 70–80% (20–30% decline) of their initial populations. The decline in the population on HJA appeared to occur during 1992–1993, whereas the decline on COA occurred during the last 4 years of the study (Fig. 9c). There appeared to be a decline in the population on the NWC study area, but precision was insufficient to detect a difference from $\lambda = 1.0$ (Fig. 9a). In contrast, populations on the KLA, TYE, CAS, and HUP study areas remained relatively stationary, as confidence intervals around the λ_ts overlapped 1.0 substantially. There were not enough years of data for MAR to assess population trends with estimates of realized population change.

DISCUSSION

This study is the fourth meta-analysis of demographic rates of northern spotted owls in the past 2 decades. The first of these analyses included only 5 study areas common to this study (OLY, TYE, HJA, CAS, NWC) and a limited number of years of data (Anderson and Burnham 1992). The major findings of that analysis were that annual survival rates of adult females had declined significantly and that populations of territorial females had declined an average of 7.5% per year from 1985 to 1991. The
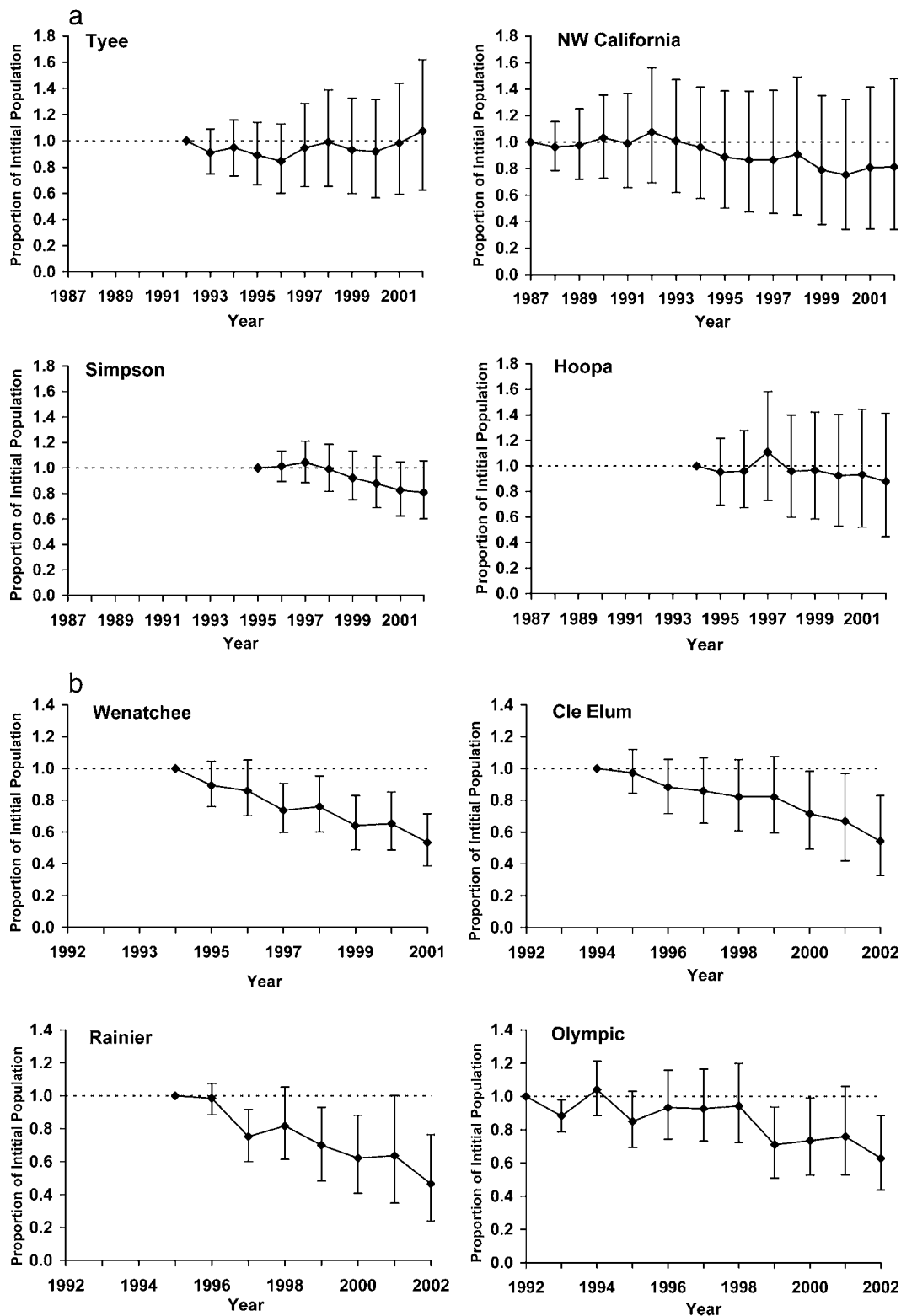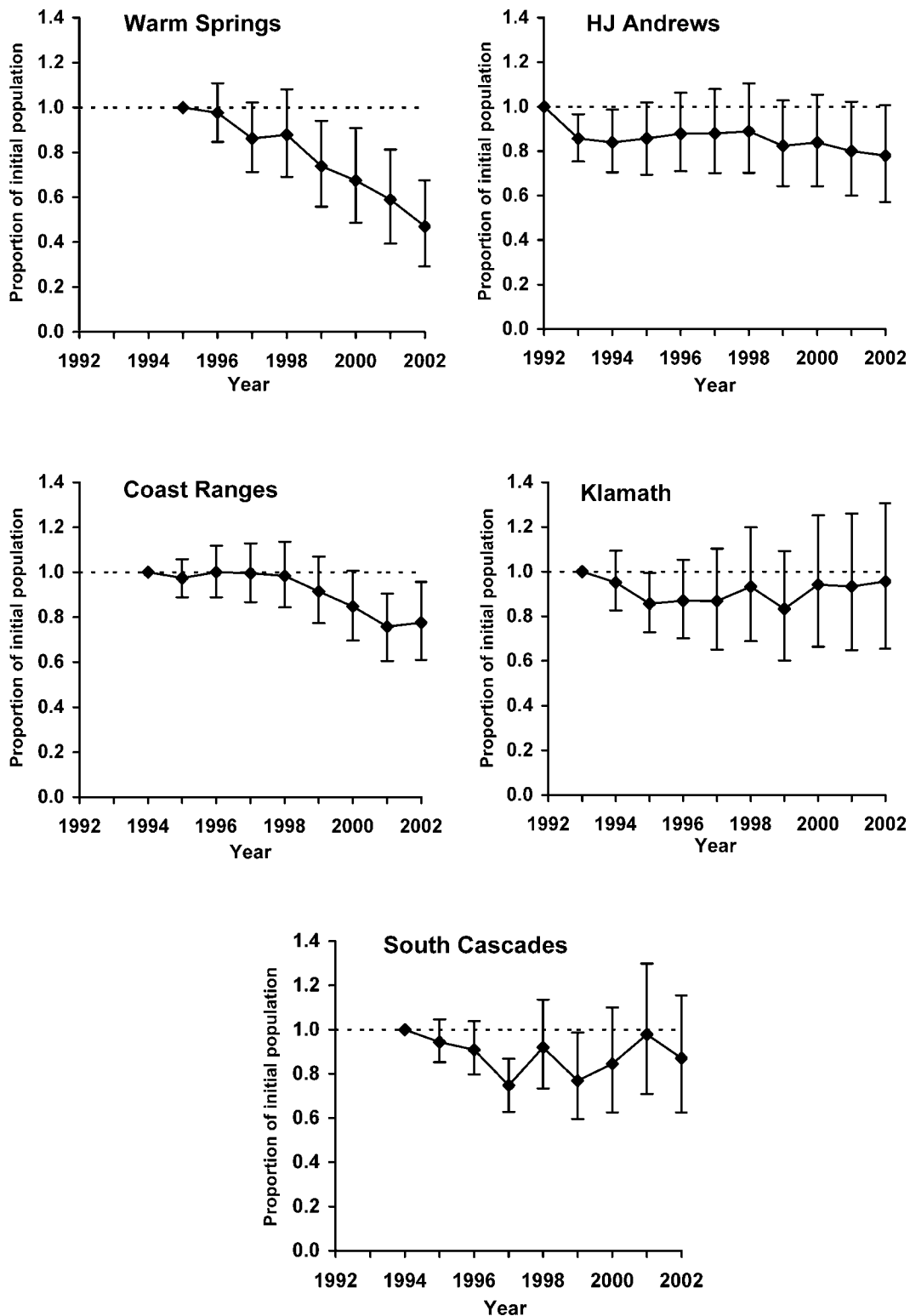
Figure 9. Estimates of realized population change, Δ_t, with 95% confidence intervals for northern spotted owls in the 4 density study areas in Oregon and California (a) and 4 territorial study areas in Washington (b).

second analysis was conducted in 1993 and included 11 study areas, 6 of which were new to the previous study (Burnham et al. 1996, Forsman et al. 1996a). The 4 major findings of the second analysis were (1) fecundity rates varied among years and age classes, with no increasing or decreasing trends over time; (2) survival rates were dependent on age, and there was a decreasing trend in adult female survival (i.e., an accelerated rate of female mortality); (3) the annual rate of population change, λ_{PM}, was significantly <1.0 for 10 of 11 areas; and (4) the average rate of population decline was 4.5% (Burnham et al. 1996). The most alarming result of the latter study

Figure 9. Continued. Estimates of realized population change, Δ_t, with 95% confidence intervals for northern spotted owls in 5 territorial study areas in Oregon (c).

was the decline in adult female survival because the population projection matrices used to estimate λ_{PM} are most sensitive to changes in adult female survival (Lande 1988, Noon and Biles 1990). The third analysis was conducted in 1998 and included 15 study areas (Franklin et al. 1999). Results of that analysis indicated that apparent survival of adult females varied among years but did not exhibit a negative trend. Thus, the negative trend in apparent survival observed by Burnham et al. (1996) had apparently stabilized during the time between the second and third meta-analyses. Fecundity also varied among years but did not exhibit any

consistent linear trend (Franklin et al. 1999). Based on estimates of demographic parameters averaged across study areas, Franklin et al. (1999) estimated an overall λ_{PM} of 0.961 (Leslie matrix models), which indicated a 3.9% decline per year in the population of territorial females. This estimate included an adjustment to juvenile survival rates due to emigration, which was based on a sample of radio-marked juveniles from 3 study areas (see Forsman et al. 2002).

Coincident with the release of the results of the first 2 meta-analyses, the final draft recovery plan for the northern spotted owl was released (U.S. Department of Interior 1992). The final draft recovery plan was soon followed by the Northwest Forest Plan, which was developed to conserve habitat for spotted owls and other species of plants and animals associated with late-successional forests (FEMAT 1993, U.S. Department of Agriculture and U.S. Department of Interior 1994). The reserve design of the Northwest Forest Plan excluded large areas of late-successional forests from timber harvest and provided an ad hoc test of the effect of habitat preservation on population trends of spotted owls. Although no cause and effect could be established, results from the third demographic analysis indicated that the declining trends in owl populations and adult female survival in earlier analyses were reduced or stabilized (Franklin et al. 1999).

Before we provide an overview of the results of this study, we must ask, What is the frame of reference, and what kind of inferences can be made from the results of the present study? From a statistical standpoint, a formal inference can be made only from the sample of marked and recaptured owls to the population of owls on the study areas in which the marked owls were located. Although the 14 study areas covered a large latitudinal and elevational gradient, they were not selected randomly. Consequently, our results cannot be considered representative, by virtue of the study design, of demographic trends of northern spotted owls throughout their entire range. For example, there were no study areas in the northern Coast Range of Oregon, the coastal mountains of southwestern Washington, or the California Cascades province. However, spotted owl populations in those areas were so low that demographic studies of the type we report here would not be possible. Nevertheless, our 14 study areas were large and covered much of the geographic range of northern spotted owls, including a variety of landownerships (private, tribal, mixed private and federal, federal lands) and management strategies. Boyce et al. (2005) speculated that these study areas have the best spotted owl habitat and vital rates and thus the highest populations of spotted owls. In contrast to their speculations, the amount of spotted owl habitat in 9 of the 14 study areas was very similar ($<\pm5\%$) to that on federal lands surrounding the study areas (Appendix F). Two of the remaining 5 areas were national parks (OLY, MAR), and, as expected, they had more (+13 and +14%, respectively) owl habitat than federal lands surrounding them. The HUP study area was located on tribal lands and had 15% less owl habitat than surrounding federal lands. The SIM study area was on private land and had 14% more owl habitat than adjacent federal lands. In addition to these similarities, the amount of owl habitat in the study areas was above that for which others have found depressed productivity (Bart and Forsman 1992, Franklin et al. 2000) or apparent survival rates

(Franklin et al. 2000, Olson et al. 2004). Consequently, we believe that our results are representative of most populations of northern spotted owls on federal lands. Because management practices on state and private lands vary widely, they have less owl habitat (Appendix F), and because our coverage of those lands was less extensive, our results likely were not applicable to all of these lands. In the following sections, we discuss the status and trends in fecundity, apparent survival, and annual rate of population change. This is followed by a discussion of some of the characteristics of spotted owl populations on the individual study areas and possible causes for the recent population declines.

Fecundity

Our results indicate that there was substantial annual variation in fecundity in most study areas with a biennial cycle of high fecundity in even-numbered years and low fecundity in odd-numbered years. However, this cycle was not apparent in at least 4 study areas, and it waned in the latter years of the study. There also were differences among age classes with highest fecundity for adult ($>$3-year-old) owls, lower fecundity for 2-year-olds, and very low fecundity for 1-year-old owls. In addition, we found that time trends in fecundity rates varied among study areas. Fecundity was slightly increasing in TYE and HUP; stable in RAI, OLY, WSR, HJA, KLA, and MAR; and decreasing in WEN, CLE, COA, CAS, NWC, and SIM (Table 21). Our meta-analysis of NYF also indicated differences among regions and substantial annual variability with no apparent time trend. Spotted owls in the mixed-conifer region of Washington (CLE, WEN) had the highest fecundity rates, and those in the Douglas-fir region of the Oregon Coast had the lowest fecundity rates. We suspect that this variation among areas was due to regional or local variation in weather and prey abundance, but an analysis of these effects was beyond the scope of this study.

The high temporal variability in fecundity and the biennial cycle of high and low years was consistent with results of previous meta-analyses on northern spotted owls (Burnham et al. 1996, Franklin et al. 1999). High temporal variability in fecundity is a common life history trait of long-lived species (Gaillard et al. 1998, Pfister 1998), and such variability, coupled with low variability in survival, is predicted by a "bet-hedging" life history strategy (Franklin et al. 2000). This high temporal variability in fecundity also is typical of reproductive patterns in many species of owls in the northern hemisphere (Houston and Francis 1995, Rohner et al. 1995, Rohner 1996, Brommer et al. 2002). Temporal variability in fecundity was probably related to climatic factors, prey abundance, or both (Franklin et al. 2000, Rosenberg et al. 2003). Climatic models explained all the temporal variation in fecundity in a population of northern spotted owls in northern California (Franklin et al. 2000), which was due to a negative effect of precipitation on reproductive output during the late nesting period. Other studies of northern spotted owls have found a negative relation between precipitation during the preceding fall and winter (Wagner et al. 1996) or during the nesting season (Zabel et al. 1996, Olson et al. 2004) on fecundity. Mean fledgling production was negatively correlated with precipitation during the nesting season for California spotted owls in both oak woodlands and conifer forests (North et al. 2000). In contrast, reproductive output of Mexican spotted owls (*S. o. lucida*) in the xeric regions of Arizona and New Mexico was positively

Table 21. Summary of trends in demographic parameters for northern spotted owls from 14 study areas in Washington, Oregon, and California, 1985–2003.

Study area[a]	Landownership[b]	Fecundity	Apparent survival	λ_{RJS}	Δ_t[c]
Washington					
WEN	Mixed	Declining	Declining	0.917	Declining
CLE	Mixed	Declining[d]	Declining?[e]	0.938	Declining
RAI	Mixed	Stable	Declining	0.896	Declining
OLY	Federal	Stable	Declining	0.956	Declining
Oregon					
COA	Mixed	Declining?[d]	Stable	0.968	Declining
HJA	Federal	Stable?[f]	Stable	0.978	Declining
WSR	Tribal	Stable	Stable	0.908	Declining
TYE	Mixed	Increasing	Stable	1.005	Stationary
KLA	Mixed	Stable	Stable	0.997	Stationary
CAS	Federal	Declining	Stable	0.974	Stationary
California					
NWC	Federal	Declining	Declining	0.985	Declining?[g]
HUP	Tribal	Increasing	Stable	0.980	Stationary
SIM	Private	Declining[d]	Stable	0.970	Declining
MAR	Federal	Stable	Stable	NA[h]	NA[h]

[a] WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.
[b] Mixed ownership indicates areas with a mixture of federal and private lands, and federal ownership indicates areas in which most lands were administered by the U.S. Forest Service, U.S. Bureau of Land Management, or U.S. National Park Service.
[c] Trend based on estimates of realized population change (Δ_t).
[d] Best model included age and even-odd year effects, but a competing model had a negative time effect on productivity.
[e] Variable among years, but with a declining trend.
[f] Decreasing in early years, increasing in last 5 years, but stable overall.
[g] Gradual declines in fecundity and apparent survival, plus estimates of realized population change suggest a decline in last 8 years.
[h] Sample too small to estimate λ.

related to the amount of precipitation during the monsoon season in the previous year (Seamans et al. 2002). This response likely was due to an increase in plant growth that resulted in an increase in mammalian prey (Seamans et al. 2002). The findings of the above studies suggest that the increased frequency of El Niño events may have had an effect on demography of northern spotted owls over the past 2 decades.

The potential influence of prey abundance on annual variation in fecundity in northern spotted owls has not been well studied. In the Oregon Cascade Mountains, Rosenberg et al. (2003) found a positive correlation between fecundity of northern spotted owls and the abundance of deer mice (*Peromyscus maniculatus*) during the nesting season; however, deer mice were not the most important prey in spotted owl diets, so this might not have been a cause-and-effect relationship. Similarly, Ward and Block (1995) described a year of high reproduction by Mexican spotted owls in southern New Mexico that was associated with an irruption of white-footed mice (*P. leucopus*), one of their primary prey species. The relation of spotted owl reproduction to prey abundance needs further study throughout the range of the species.

The effects of female age on fecundity of northern spotted owls has been well documented (Burnham et al. 1996, Franklin et al. 1999) with older females occupying most of the territories and responsible for most of the breeding in any given year. Our estimates of mean fecundity for 1- and 2-year-olds and adults ($\bar{x}$ = 0.074, 0.208, 0.372, respectively) were similar to those ($\bar{x}$ = 0.068, 0.205, 0.339, respectively) reported by Burnham et al. (1996) for many of the same study areas. Similar differences in fecundity among age-groups have been reported for California spotted owls (Blakesley et al. 2001) and Mexican spotted owls (Seamans et al. 1999, 2001). Our estimate of mean adult fecundity ($\bar{x}$ = 0.372, SE = 0.029) was comparable to estimates for other spotted owl populations. For example, estimates of mean fecundity for the California spotted owl include 0.291 (SE = 0.33) for Lassen National Forest (Blakesley et al. 2001) and 0.400 (SE = 0.005) for the Eldorado National Forest (Seamans et al. 2001). Mean fecundity estimates for adults from 2 populations of Mexican spotted owls were 0.494 (SE = 0.022) and 0.380 (SE = 0.019) (Seamans et al. 1999). The highest adult fecundity rates in our study were 0.574 (SE = 0.069), 0.530 (SE = 0.056), and 0.491 (SE = 0.058) for the CLE, MAR, and WEN study areas, respectively. CLE and WEN were in mixed-conifer forests east of the Cascade crest in Washington, and fecundity for these 2 areas were the highest rates recorded for northern spotted owls. The reasons for these high fecundity rates in mixed-conifer forests of Washington may include a higher diversity or biomass of prey. For example, Lehmkuhl et al. (2006) found higher abundance of northern flying squirrels on the eastern slope of the Cascade Mountains in Washington than was reported by studies in Oregon (Carey et al. 1992, Rosenberg and Anthony 1992) or western Washington (Carey et al. 1992). The higher fecundity of spotted owls in eastern Washington also may be a compensatory response to lower survival rates on these areas (see below). The high fecundity rates for MAR are believed to be due to consistent breeding success among years (no even-odd year fluctuations), mild weather, and abundant prey (Willy 1992).

Contrary to our a priori hypothesis, there was no evidence for a negative effect of barred owls on spotted owl fecundity. In

contrast, Olson et al. (2004) found a negative effect of barred owls on fecundity of spotted owls with a territory-specific approach for the TYE study area. Kelly (2001) found little evidence that fecundity of spotted owls was influenced by the presence of barred owls. However, she qualified her results by pointing out that studies like hers may underrepresent the impact of barred owls on fecundity of spotted owls if spotted owls are displaced by barred owls, go undetected, and cannot breed because they lost their territories. In addition, the covariate we used for the effect of barred owls was a coarse-scaled, year-specific variable that lacked the specificity to individual territories that may be necessary to fully evaluate the effect of barred owls on spotted owl fecundity. This, along with the small sample of barred owls on study areas in California, may account for some of the counterintuitive results we observed, particularly the positive relation between barred owls and fecundity in 2 of the California study areas.

All studies of fecundity are subject to biases that result from behavioral attributes of the species or methodological problems. For spotted owls, the biggest potential for bias occurs when we cannot find an individual or pair in a given year and they are recorded as "missing data." If these missing pairs nested successfully, then we have underestimated fecundity. On the other hand, some of missing pairs may have been present and not reproducing, in which case we would have overestimated fecundity. We have no way of knowing which one of these scenarios is most prevalent in a given year, but we suspect that the latter one is the more frequent case. Regardless, we believe that the biases in the estimates of fecundity in this study were minimal because our recapture probabilities were high, and the frequency of missing data in most years was small (<10%). Any biases certainly did not affect our ability to detect even-odd year fluctuations, differences among age classes, and time trends in fecundity in this study, which were the primary objectives for the analysis of the NYF. Had our primary interest in fecundity data been to estimate annual rate of population change, λ_{PM}, with Leslie matrix models, any biases in the estimates of fecundity would be of more concern.

Apparent Survival

Our analyses of data from individual study areas indicated that apparent survival rates differed among age classes for most areas, were declining on 5 (WEN, CLE, RAI, OLY, NWC) of the 14 areas (Table 21), and were negatively associated with the presence of barred owls on 2 (WEN, OLY) areas. Apparent survival of males and females were similar throughout most of the range of the subspecies except for the MAR study area in California. In the meta-analysis of apparent survival, we found differences among ecological regions and changes over time with a downward trend in apparent survival in the mixed-conifer and Douglas-fir regions of Washington. The meta-analysis also indicated a negative correlation between NYF and survival rates the following year (discussed in more detail below), but this effect was limited to the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir region of the Oregon Cascade Mountains.

Estimates of apparent survival of territorial owls in our study ranged from 0.750 to 0.913 for adults, 0.626 to 0.890 for 2-year-olds, and 0.415 to 0.817 for 1-year-olds. These survival rates were generally comparable to those reported by Burnham et al. (1996)

and Franklin et al. (1999) for some of the same study areas at an earlier date. Estimates of apparent survival of adult California spotted owls on 5 areas (Franklin et al. 2004) ranged from 0.813 to 0.877 (SE = 0.015–0.020) and were similar to ours. Our estimates of adult survival were comparable to or higher than estimates for adult California spotted owls in Lassen National Forest ($\bar{x} = 0.827$, SE = 0.008; Blakesley et al. 2001) and Eldorado National Forest ($\bar{x} = 0.795$, SE = 0.006; Seamans et al. 2001, Franklin et al. 2004) and for adult Mexican spotted owls in Arizona ($\bar{x} = 0.814$, SE = 0.003) and New Mexico ($\bar{x} = 0.832$, SE = 0.015; Seamans et al. 1999). Our results and those of the authors above indicate that spotted owls have evolved a life history strategy throughout their range of high adult survival with low annual variability, coupled with high annual variability in fecundity. Because spotted owls inhabit variable environments, high survival rates allow individuals to retain territories and persist through periods of less favorable conditions to reproduce in later years. This strategy has been referred to as "bet hedging," where natural selection favors adult survival at the expense of present fecundity if recruitment of offspring is unpredictable from year to year (Stearns 1976, Franklin et al. 2000). High adult survival is also important because sensitivity analyses on population dynamics of northern spotted owls indicate that annual rates of population change are most influenced by changes in adult survival (Noon and Biles 1990, Lande 1991, Blakesley et al. 2001).

Our results indicated that apparent survival rates were stable on 9 study areas (COA, HJA, WSR, TYE, KLA, CAS, HUP, SIM, MAR) but declining on 5 study areas (WEN, RAI, OLY, CLE, NWC; Table 21). Results of the meta-analysis also indicated a significant decline in survival in the mixed-conifer and Douglas-fir regions of Washington, which included the WEN, CLE, OLY, and RAI study areas. Declining survival rates were reported in a meta-analysis for some of these same populations in an earlier study (Burnham et al. 1996), but these declines appeared to have stabilized in a more recent meta-analysis (Franklin et al. 1999). The reasons for these declines in apparent survival are not readily apparent but may include loss of habitat due to timber harvest or wildfire, changing weather patterns, declines in prey abundance, and/or increasing competition with barred owls (see below).

Potential Biases in Estimates of Apparent Survival.—The potential biases in the estimates of survival rates for northern spotted owls would include those resulting from temporary and permanent emigration, heterogeneity in capture probabilities, and band loss. If estimates of apparent survival were used for true survival (e.g., in a Leslie matrix), then permanent emigration would result in bias in estimates of true survival. There are other potential biases in estimating survival rates, but these would be the primary ones to consider for this species under the conditions of our capture–recapture studies. Some of these topics have been investigated extensively by Manly et al. (1999) with data for spotted owl populations on the WEN study area using computer simulations of 6 and 10 years and 260 and 420 marked individuals, respectively. They found that variation in capture probabilities for nesting and nonnesting owls, temporary emigration, and dependent captures of both members of nesting pairs had little effect on survival estimates. They also found that a model close to the simulated model was selected for capture and survival probabilities

when QAIC was used for model selection. In addition, the combination of high recapture and survival probabilities found in this study likely reduced any bias that may have been associated with heterogeneity of recapture probabilities (Carothers 1973, 1979; Pollock et al. 1990; Hwang and Chao 1995).

With respect to permanent emigration, investigations on some of these same study areas (Forsman et al. 2002) found that only 6.6% of resident owls dispersed from their territories, and most merely moved to an adjacent territory and did not disappear from the study area. These data suggest that permanent emigration was usually <2–3% per year for territorial owls. Consequently, we believe that our estimates of apparent survival were close to true survival because permanent emigration had little effect on our estimates of apparent survival of nonjuvenile, territorial spotted owls. Lastly, we have seen little evidence of band loss in this species. All owls are double-marked because we typically place a U.S. Fish and Wildlife Service band on one leg and a colored band on the other leg. There were only 2 cases where colored bands were lost and no cases where U.S. Fish and Wildlife Service bands were lost from over 6,000 banded owls in a previous study (Franklin et al. 1996); therefore, the loss of both bands was zero in these studies. Occasionally, colored bands faded on older owls, but these individuals were captured and their bands replaced when this occurred. In summary, we believe that any biases in our estimates of apparent survival were minimal based on the above assessments, the large number of owls banded, and the length of most of our studies.

Annual Rate of Population Change (λ)

Our decision to use the reparameterized Jolly–Seber method (Pradel 1996) to estimate annual rates of population change (λ_{RJS}) was a departure from most demographic analyses on northern spotted owls (Anderson and Burnham 1992, Burnham et al. 1996), California spotted owls (LaHaye et al. 1992, Blakesley et al. 2001), and Mexican spotted owls (Seamans et al. 1999, 2002). Consequently, our results are most comparable to those of Franklin et al. (1999, 2004), who also used the reparameterized Jolly–Seber method. Most of the earlier studies used Leslie matrix models to estimate λ_{PM} (Caswell 2000), but these estimates were likely biased low (Raphael et al. 1996). This bias was due to the fact that estimates of juvenile survival for northern spotted owls from Cormack–Jolly–Seber open population models are negatively biased (Raphael et al. 1996) because emigration is confounded with mortality in estimates of apparent survival, and it is well known that juvenile spotted owls often disperse long distances from their natal areas (Forsman et al. 2002). For this reason and others mentioned in the Methods section (see also Franklin et al. 2004, Boyce et al. 2005), we used only λ_{RJS} to estimate the annual rate of population change.

Point estimates of λ_{RJS} for the individual study areas were <1.0 for all areas except TYE. We found strong evidence that spotted owl populations on the WEN, CLE, WSR, and SIM study areas were declining during the period of study. There also was evidence that populations were declining on the RAI, OLY, COA, and HJA areas as well because 95% confidence intervals barely included 1.0. Estimates of realized population change illustrate that populations on all the above 8 study areas declined from the initial numbers of territorial owls at the start of the study, and

some of the declines were as much as 40–50% over the past decade. Populations were relatively stationary on the TYE, KLA, CAS, and HUP study areas as a result of high survival and fecundity rates, which were stable over the period of study (Table 21). The status of the owl population on the NWC study area was somewhat questionable; we found slight decreases in fecundity and apparent survival on this area, suggesting population declines, but estimates of λ_{RJS} and realized population change lacked the precision to detect any small declines that may have occurred. Our estimate of mean λ_{RJS} for the 13 study areas was 0.963 (SE = 0.009), which suggested an average population decline of 3.7% per year during the study. These results were consistent with the recent declines in apparent survival in many of the study areas and declines in fecundity in 6 of the areas. This is a higher rate of decline than was reported in a previous analysis (λ_{RJS} = 0.997, SE = 0.043; Franklin et al. 1999), which included many of the same study areas as our analyses.

A demographic analysis of 5 California spotted owl populations (Franklin et al. 2004) indicated that the estimates of λ_{RJS} were not significantly <1.0 and that populations were, therefore, stationary. However, Franklin et al. (2004) stated that estimates of population change in their study were "not sufficiently precise to detect declines" if they occurred. Estimates of λ_{RJS} in our study were reasonably precise for most study areas; coefficients of variation ranged from 1.2 to 6.1%. Coefficients of variation in this study were >5% for only 1 study area (RAI = 6.1%). As a result, the estimate of λ_{RJS} for RAI had a wider confidence interval and lacked the precision to detect a difference from λ_{RJS} = 1.0. Although estimates of temporal process variation were high for the CAS, TYE, and WEN study areas, 95% confidence intervals for all study areas overlapped considerably, and all the intervals included zero. The rate of population change from the meta-analysis was constant for the 4 density study areas. In contrast, estimates of population change from the meta-analysis for the territory-specific study areas were not constant, as the rate of population change varied considerably over time and among the 9 territorial study areas.

Our estimates of λ_{RJS} apply only to the years from which data were analyzed, approximately 1990–2003; therefore, any predictions about past or future trajectories of these populations are not recommended. In addition, estimates of λ_{RJS} indicate the average annual rate of population change in the number of owls on each study area. For example, estimates of λ_t that were <1.0 represented a decrease in the number of owls; however, subsequent values of λ_t > 1.0 for these populations did not necessarily indicate that the population had increased to its original numbers. They merely indicated that numbers had increased relative to the number of owls the previous year. Consequently, a fluctuating pattern in λ_t can exist that ultimately results in losses or gains in the number of owls, which would be reflected by the mean λ_{RJS} over time for each area. We attempted to understand how changes in λ_t were related to trends in populations over time by estimating realized changes in populations, Δ_t, for each study area. Based on these estimates, spotted owl populations on the WEN, CLE, RAI, and WRS study areas declined 40–60% during the study, and populations on the OLY, HJA, COA, and SIM study areas declined by 20–30%. The population on the NWC study area

appeared to have declined about 15%, but the precision of this estimate was too low to detect a significant decline. Populations on the remainder of the areas (TYE, KLA, CAS, and HUP) were approximately stationary during the period of this study. The number of populations that have declined and the rate at which they have declined are noteworthy, particularly the precipitous declines on the 4 Washington study areas and WSR in Oregon.

Bias in Estimating Goodness of Fit and Overdispersion.— There are potential biases in the estimator of overdispersion, c, when the estimate is based on the global goodness-of-fit statistic. Any such bias affects the precision of apparent survival, ϕ, and annual rate of population change, λ, and this is particularly germane to the computation of confidence intervals for λ_{RJS}. For any data set, the overall chi-square statistic (T) for goodness of fit reflects all departures from a perfect fit to the global model. These components of lack of fit (LOF) are additive and comprised of identifiable outliers (O), structural lack of fit (S), and pure overdispersion (C). The effect on bias and variance of parameter estimates depends on the nature of the lack of fit. Outliers and structural lack of fit may result in bias but not inflated variance. Overdispersion results in inflated variance, but it does not cause bias. Consequently, our estimator of the variance inflation factor, c, is biased upward by the inclusion of outliers (O) and structural lack of fit (S) in T. Unfortunately, we cannot isolate or remove the structural lack of fit from this statistic, but we can identify gross outliers (i.e., capture histories such as 01100000000101) and remove their contribution to T. The result of computing such an adjusted T, even when there are few outliers, can be a noticeable reduction in the estimate of c (e.g., from 1.9 to 1.4). We did not use such an improved estimator of overdispersion in our analyses because this issue was not discussed as part of the analysis protocol, and we did not appreciate a priori the effect that even a few outliers could have on the estimate of c. Consequently, our estimates of overdispersion, c, are biased high, and, as a result, so are our variance estimates and confidence interval lengths for ϕ and λ. This means that we have been conservative in assessing the precision of ϕ and the status of populations from the estimation of λ_{RJS} and their 95% confidence intervals.

Effects of Barred Owls

We hypothesized that barred owls would have a negative effect on demographic rates of spotted owls because barred owls are morphologically and ecologically similar to spotted owls, and there is evidence for competitive interactions between these 2 species (Herter and Hicks 2000, Kelly et al. 2003, Pearson and Livezey 2003, Olson et al. 2005). Contrary to our hypothesis, we found little evidence for an effect of barred owls on fecundity of spotted owls, although the results suggested a negative effect for WEN and OLY. In contrast, there was some indication that barred owls may have had a negative effect on survival rates of spotted owls, but this was specific to 3 study areas in Washington. In the meta-analysis of all 14 study areas, we found evidence of a negative effect of barred owls on spotted owl survival for the WEN and OLY study areas; in addition, this effect was close to being significant for CLE. Similarly, the results for individual study areas indicated a negative effect of barred owls on spotted owl survival for the OLY and WEN study areas with the effect for CLE being suggestive. These results provide some evidence

that barred owls may have had a negative effect on apparent survival of spotted owls or caused them to emigrate from their territories in the northern part of the spotted owl's range. This is the portion of the spotted owl's range where barred owls have been present the longest and are most abundant (Appendix B) and where populations of spotted owls are doing the poorest. We found little evidence for an effect of barred owls on survival of spotted owls in Oregon. Kelly (2001) and Olson et al. (2005) found that barred owls were having a negative effect on occupancy of territories by spotted owls in Oregon but not reproduction. The occurrence of barred owls in spotted owl territories in California was quite low (<5%), so we doubt that they were having an effect on the 4 study areas in California. Nonetheless, barred owls have been increasing their geographic range southward and are becoming more abundant throughout most of the range of the northern spotted owl (Kelly et al. 2003), so their effect on spotted owl populations should be monitored closely in the future.

Many of us were of the opinion that barred owls were having more of an effect on occupancy of territories (a population parameter that we did not analyze) by spotted owls than fecundity or survival. This observation was consistent with previously published reports that have documented a negative influence of barred owls on occupancy of territories by spotted owls (Kelly et al. 2003, Pearson and Livezey 2003, Olson et al. 2005). If this is indeed true, this displacement is likely a form of interference competition (Connell 1983). In order to investigate the potential effect of barred owls on spotted owls in the future, any covariate for the occurrence of barred owls should be territory specific as well as time specific, and analyses should investigate the effects on occupancy as well as fecundity and survival. The barred owl covariate that we used in this study was not site specific, so our results cannot be considered definitive. The recent methods of MacKenzie et al. (2002, 2003), which incorporate probabilities of detection, could be used to estimate occupancy, colonization, and extinction rates of 1 or both species (Olson et al. 2005). This type of analysis is needed to assess the influence of barred owls on spotted owls in the future.

Correlation Between Reproduction and Apparent Survival Rates

Our meta-analyses of apparent survival of spotted owls indicated a negative correlation between survival rates and NYF in the Douglas-fir and mixed-conifer regions of Washington and the Douglas-fir region of Oregon. We found no significant correlations for the Oregon Coast Range, southern Oregon, and California regions. The regions where we found the negative correlations were the more northern or higher elevation areas among our study areas. We also found that fecundity was highest during even-numbered years for most study areas (Fig. 2) followed by low survival on all areas the following year (Fig. 5). These negative correlations between annual fecundity and apparent survival on some study areas suggest that (1) there was a cost of reproduction or (2) there was some other ultimate factor(s) influencing fecundity and survival of owls. The cost of reproduction on body condition of birds has been documented (Maigret and Murphy 1997, Golet and Irons 1999, Hanssen et al. 2003), and there is evidence that reproduction can have a negative

effect on survival of western gulls (*Larus occidentialis*; Pyle et al. 1997), greater flamingos (*Phoenicopterus ruber*; Tavecchia et al 2001), great tits (*Parus major*; McCleery et al. 1996), and lesser scaup (*Aythya affinis*; Rotella et al. 2003). Consequently, a cost of reproduction is a possible explanation for the negative correlations we observed between fecundity and survival. Our assessment of the cost of reproduction may be conservative because hetero-geneity in individual owl or territory quality may create a positive correlation between fecundity and survival. That is, high-quality individuals or territories may have both higher survival and greater reproductive success than poor-quality individuals or territories. Such a positive correlation could mask the expected negative correlation between survival and NYF under a cost-of-reproduc-tion scenario.

In addition, past research on spotted owls has shown that cold, wet winters or springs can have a negative effect on fecundity of northern spotted owls in southern Oregon (Wagner et al. 1996, Zabel et al. 1996) and on both fecundity and survival in northern California (Franklin et al. 2000) and the Coast Range of Oregon (Olson et al. 2004). Because winter weather is more severe in northern regions and high elevations, where we saw the potential effect of reproduction, this may indicate that the effects of winter weather on fecundity and/or survival may be an important factor also. Consequently, the cost of reproduction on survival of spotted owls in the northern regions may be driven ultimately by winter and/or spring weather patterns. Since our covariate for NYF in this analysis was year specific, this phenomena needs to be studied further with site-specific covariates and at the individual study area.

Possible Causes of Population Declines

Assessment of the possible causes of population declines was beyond the scope of this study because the potential causes were numerous, and we were unable to develop comparable covariates for the analyses of fecundity, survival, and population change for all study areas. Consequently, we can only speculate about possible causes of population declines.

Based on estimates of λ_{RJS} and realized population change (Δ_t), there was strong evidence for declines in populations on the WEN, CLE, OLY and RAI study areas in Washington and the WSR, HJA, and COA study areas in Oregon. These population declines were due, at least in part, to the declines in apparent survival on some of these study areas, particularly those in Washington. Reasons for these declines in survival and popula-tions were unknown but may include, but are not limited to, the following: (1) the high density of barred owls on study areas in Washington and parts of Oregon (Herter and Hicks 2000, Kelly 2001, Pearson and Livezey 2003), (2) loss of habitat due to wildfire, (3) harvest of spotted owl habitat, (4) poor weather conditions, and (5) forest defoliation caused by insect infestations (Hummel and Agee 2003). For example, large areas of spotted owl habitat on private land in the CLE study area were harvested from 1990 to 2003, and large areas in the WEN study area were impacted by wildfires during the same period (Gaines et al. 1997). Because spotted owls are a long-lived species and large amounts of their habitat were harvested during the 1980s, some of the declines during our study may have been due to "lag effects" from the loss of habitat during that time. In contrast to WEN and

CLE, RAI is comprised mostly of federal lands, and there was little timber harvest or wildfire on this area during the study, yet populations on this area declined also. The reason for the decline on the WSR study area was partly due to loss of habitat, as there has been continued logging of old forests in the area over the past 2 decades, and there have been wildfires in some nesting territories. The decline on the HJA area occurred during 1992–1993 before barred owls became very abundant, and there also has been very little habitat loss due to timber harvest or wildfire on this area. Consequently, the possible causes of declines on HJA are unknown but may include poor weather conditions and/or declining prey abundance. Population declines on the COA area occurred from 1999 to 2002 and may be the result of continued harvest of owl habitat on private lands within the area and the gradual increase in barred owls. The evidence for declining populations of spotted owls in the northernmost study areas in Washington and Oregon may indicate an effect from barred owls, which were more abundant in Washington and northern Oregon (Appendix B). The cause of this range expansion is unknown, but it was likely triggered by gradual changes in climate and vegetation. In contrast, we suspect that barred owls had little influence on demography of spotted owls in California because they were uncommon in those study areas.

The slight declines in fecundity and apparent survival on NWC in California have likely caused a slow but gradual decline in owl populations in that area. The reasons for this decline are not clear because there has been little loss of habitat in the area and barred owls were relatively uncommon during our study. In contrast, we suspect that the 3% annual decline in the SIM study area was likely due to habitat loss. Lands in the SIM study area were privately owned and were subjected to active management during our study, which included harvest of spotted owl habitat under a federally approved Habitat Conservation Plan. Data from the SIM area were important to our analyses because the land was privately owned, and this was the only long-term demographic study within the coastal redwood zone of California

Populations in the TYE, KLA, CAS, and HUP study areas were stationary during the study (Table 21), which was a result of high, stable, or increasing rates of survival and fecundity. The TYE and KLA study areas included a mixture of federal (Bureau of Land Management) and private lands, and there was considerable harvest of young and mature forests on private lands in these areas during our study. In contrast, there was only minimal harvest of mature and older forests in the CAS study area, which was mostly federal land. The relative stability of spotted owl populations in HUP was particularly interesting because old forests were harvested in that area during our study. However, the forest management plan for the Hoopa Reservation did not allow intensive clear-cut logging, and 30% of the forested lands were retained as old-forest reserves in riparian protection zones, tribal reserves, and spotted owl core nesting areas. Selective logging was used throughout most of the Reservation, and some large trees were retained in all harvest units.

Status of Owls on the 8 Monitoring Areas

The status of northern spotted owl populations on the 8 monitoring areas (CLE, OLY, TYE, HJA, COA, KLA, CAS, NWC) was of special interest to federal agencies because these

areas were established to monitor population trends of the species under the NWFP (Lint et al. 1999). These study areas are comprised of federal (U.S. Forest Service, National Park Service) or mixed private and federal lands (Bureau of Land Management), and portions of these study areas were managed as late-successional forest reserves for spotted owls and other species associated with older forests (FEMAT 1993). Consequently, we predicted that demographic rates of spotted owl populations would be higher on these areas than on other areas. Although populations in 4 (CLE, OLY, COA, and HJA) of the 8 monitoring areas appeared to be declining, the weighted mean $\hat{\lambda}_{RJS}$ for the 8 monitoring areas was 0.976 (SE = 0.007) compared to 0.942 (SE = 0.016) for the other areas. This indicated a 2.4% population decline per year for the 8 monitoring areas compared to a 5.8% decline per year on the other areas. Although the overall estimate of λ_{RJS} was higher for the 8 monitoring areas, the negative trends in fecundity and survival on some of these areas were cause for concern.

SUMMARY AND RECOMMENDATIONS

Our objectives were to determine if there were trends in apparent survival and fecundity rates across the range of the northern spotted owl and to determine if populations were increasing, decreasing, or stationary (Lint et al. 1999). Our 14 study areas were large in size, encompassed a significant portion of the northern spotted owl's geographic range, included a variety of landownerships and management strategies, and spanned a relatively large number of years. Our analyses also indicated that the amount of spotted owl habitat in the study areas was comparable to that in the provinces surrounding them. Consequently, we believe that our results were representative of most populations of northern spotted owls on federal lands in Washington, Oregon, and California. Because sampling of state and private lands was less extensive and management practices on these lands varied widely, we were less certain that the results were generally applicable to nonfederal lands.

The 4 major findings of this study were that (1) fecundity rates were variable among the 14 study areas but declining on 6 study areas, (2) survival rates were declining on 5 study areas and stable on the remaining areas, (3) populations were declining on 9 study areas and stationary on 4 areas, and (4) the mean $\lambda_{RJS} = 0.963$ (SE = 0.009) suggested a 3.7% annual decline in territorial populations over all study areas (Table 21). Demographic performance was poorest in Washington, where there were declines in survival rates and populations in all 4 study areas (OLY, WEN, RAI, CLE). The mean λ_{RJS} for the Washington study areas was 0.930 (SE = 0.009), indicating a 7.0% annual decline. Demographic performance was generally better in Oregon, where the mean λ_{RJS} was 0.971 (SE = 0.014), indicating a 2.9% annual decline. Survival rates were stable in Oregon, but there was evidence for population declines in the WSR, COA, and HJA areas. Populations in TYE, KLA, and CAS study areas in Oregon were stationary. Spotted owl populations in California were performing slightly better than those in Oregon and much better than those in Washington. The mean λ_{RJS} for the California study areas was 0.977 (SE = 0.005), indicating a 2.3% annual decline. Fecundity was variable among the 4 study

areas in California, survival was stable on 3 areas but declining on NWC, and populations were declining on SIM.

In general, demographic rates in the 8 monitoring areas were higher than those in other study areas. Overall, populations on 13 study areas that were part of a previous meta-analysis (Franklin et al. 1999) were doing poorer than they were 5 years ago. These results emphasize the need for further monitoring of northern spotted owl populations and research on the potential causes of population declines. Consequently, we recommend the following:

1. Continued monitoring of fecundity, survival, and annual rates of population change on all the study areas and more intensive research to determine the cause(s) of population declines. The diversity of ownership, past management strategies, and ecological conditions within the 14 study areas will allow wider interpretations of the results than a more limited set of study areas.
2. Develop and investigate additional covariates to evaluate the effect of barred owls on fecundity and survival of spotted owls. Any barred owl covariate should be territory specific and should be used to look at the barred owl effect on territory occupancy as well as fecundity and survival of spotted owls.
3. Conduct more intensive studies on the competitive interactions of barred owls and spotted owls, including resource partitioning of prey, habitat, and space as well as behavioral interactions between the species.
4. Examine the effects of weather on demographic performance of spotted owls, both separately and as part of a meta-analysis. The even-odd year fluctuations in fecundity and survival suggest some underlying cause that could be related to weather patterns or prey abundance. Our results suggested there was a negative correlation between reproduction and survival rates (i.e., a cost of reproduction), and this possibility needs further study also.
5. We anticipate that the reparameterized Jolly–Seber method (Pradel 1996) will be used to estimate annual rates of population change, λ_{RJS}, in the future. Thus, it is paramount that there are no alterations in study area boundaries and that the intensity of monitoring on the study areas be consistent from year to year. Expansion of study area boundaries during the present study created some challenging modeling that was not easily handled (see meta-analysis of λ_{RJS} for the territorial study areas). Contraction of study area boundaries would create similar problems.
6. Estimates of demographic rates varied widely among the 14 study areas. This variability in demographic rates could be more fully understood if future analyses included covariates on weather patterns, vegetative characteristics, rates of habitat loss due to logging and wildfire, and territory-specific data on the presence of barred owls. This will require the development of comprehensive and accurate vegetation maps for all the study areas within the next 5 years.
7. Estimation of survival rates of juvenile spotted owls from capture–recapture data is problematic because Cormack–Jolly–Seber open population models cannot distinguish between mortality and permanent emigration. This needs further investigation.
8. Modeling of territory occupancy of spotted owls with the

models described by MacKenzie et al. (2003, 2004) has revealed some important effects of habitat characteristics and barred owls on population dynamics of spotted owls (Olson et al. 2005). This type of analyses should be applied to additional data sets on the subspecies.

Some reviewers of this manuscript urged us to make recommendations regarding management of spotted owl populations and their habitats based on our findings. We do not believe that this would be appropriate for several reasons. First, management of the northern spotted owl has been an incredibly complicated interagency effort that has led to much federal land being reserved as habitat for owls and other species (U.S. Department of Agriculture and U.S. Department of Interior 1994). Because it is not clear if additional protection of owl habitat will reverse the population declines, we think it would not be appropriate for us to propose additional management recommendations. Second, the U.S. Department of Interior, U.S. Fish and Wildlife Service, recently conducted a 5-year Status Review of the northern spotted owl, and they have the mandate and legal authority under the Endangered Species Act to evaluate the status of the species periodically. Our results were considered in their review and decision to retain the threatened status of the subspecies. Third, we could not differentiate among the effects of habitat loss, barred owls, and climate on demography of spotted owls, so we cannot say with certainty that any management strategies will be successful in halting the observed declines. Finally, some of the possible causes of the declines are natural events (e.g., weather, wildfires), so management strategies are not appropriate.

Although the northern spotted owl has been studied intensively over the past 3 decades, there are still many unanswered questions about the factors that affect its survival and fecundity rates and overall population status. Finding answers to these questions will be challenging because the species is long lived and has high site and mate fidelity, traits that have a tendency to confound interpretations of the effects of habitat alterations on the species. If we are going to be able to understand the relative influence of habitat alterations, barred owls, climate, and other factors on spotted owl populations, future analyses will need more detailed data on these factors. We strongly encourage researchers to examine these relations in their individual study areas, as the complexity of these analyses may be beyond the scope of any meta-analysis on all areas combined.

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Appendix A. Study areas included in the January 2004 analysis of demographic trends of northern spotted owls. Asterisks indicate density study areas (DSAs) in which the entire area was surveyed each year. All other study areas were territory study areas (TSAs) in which the same sample of owl territories was surveyed each year.[a]

Study area name (acronym)	Start year[b]	λ_{RJS} Start year[c]	Expansion year[d]	Landowner[e]	Region	Latitude
Washington						
Wenatchee (WEN)	1990	1992	1994	Mixed	Washington mixed-conifer	46.996
Cle Elum (CLE)	1989	1992	None	Mixed	Washington mixed-conifer	47.195
Rainier (RAI)	1992	1993	1998	Mixed	Washington Douglas-fir	47.041
Olympic Peninsula (OLY)	1987	1990	1994	Federal	Washington Douglas-fir	47.800
Oregon						
Coast Ranges (COA)	1990	1992	None	Mixed	Oregon Coastal Douglas-fir	44.381
Tyee (TYE)*	1985	1990	None	Mixed	Oregon Coastal Douglas-fir	43.468
H. J. Andrews (HJA)	1987	1990	2000	Federal	Oregon Cascades Douglas-fir	44.213
Warm Springs Reservation (WSR)	1992	1993	None	Tribal	Oregon Cascades Douglas-fir	44.938
South Cascades (CAS)	1991	1992	1998	Federal	Oregon Cascades Douglas-fir	42.695
Klamath (KLA)	1985	1991	1998	Mixed	Oregon/California mixed-conifer	42.736
California						
NW California (NWC)*	1985	1985	None	Federal	Oregon/California mixed-conifer	40.848
Hoopa Reservation (HUP)*	1992	1992	None	Tribal	Oregon/California mixed-conifer	41.051
Simpson (SIM)*	1990	1993	None	Private	California Coast	41.122
Marin (MAR)	1998	1998	None	Federal	California Coast	37.994

[a] We analyzed data through 2003 on all study areas, except that we only analyzed λ_{RJS} on the Wenatchee Study Area through 2002 because that study area was not completely surveyed in 2003.

[b] Year that mark–recapture study was started.

[c] First year that data were used for analysis of λ_{RJS}.

[d] Year that study area size was increased, if any, for analysis of λ_{RJS}.

[e] Federal = Forest Service, Bureau of Land Management, National Park Service. Mixed = federal lands mixed with inclusions of private or state lands. Tribal and private study areas were lumped together for analyses of ownership.

Appendix B. Proportion of spotted owl territories occupied by barred owls (BO covariate) used to model the effects of barred owls on the number of young fledged, apparent survival rates, and capture probabilities of spotted owls in 14 study areas in Washington, Oregon, and California.
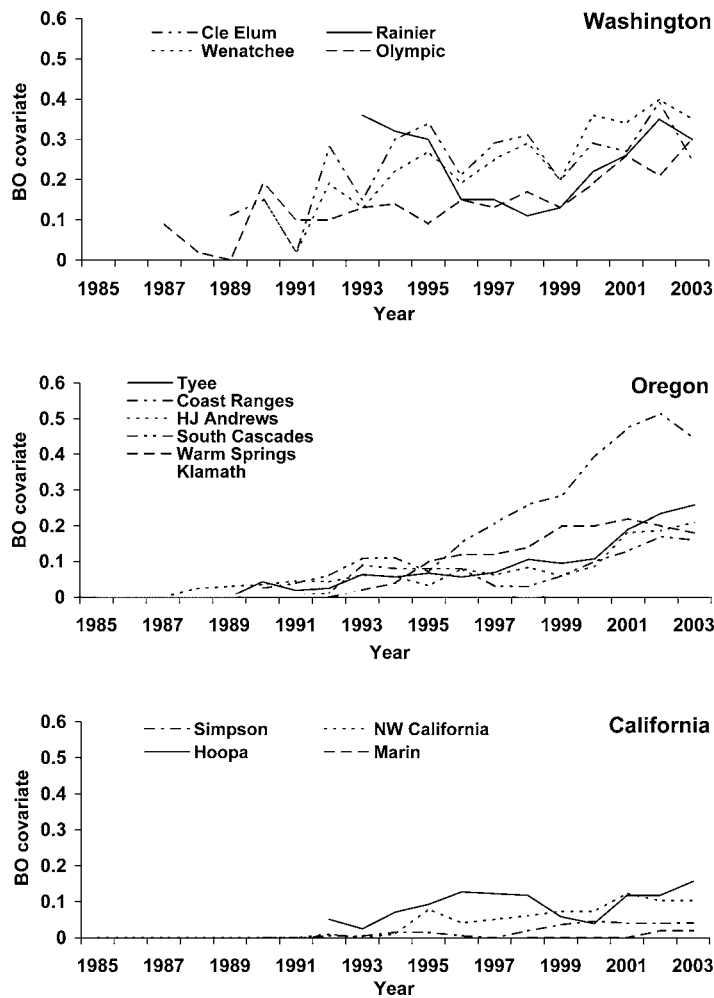
Appendix C. Reproductive covariate (no. young fledged per year) used to model northern spotted owl fecundity, survival, and capture probability on 14 study areas in Washington, Oregon, and California.
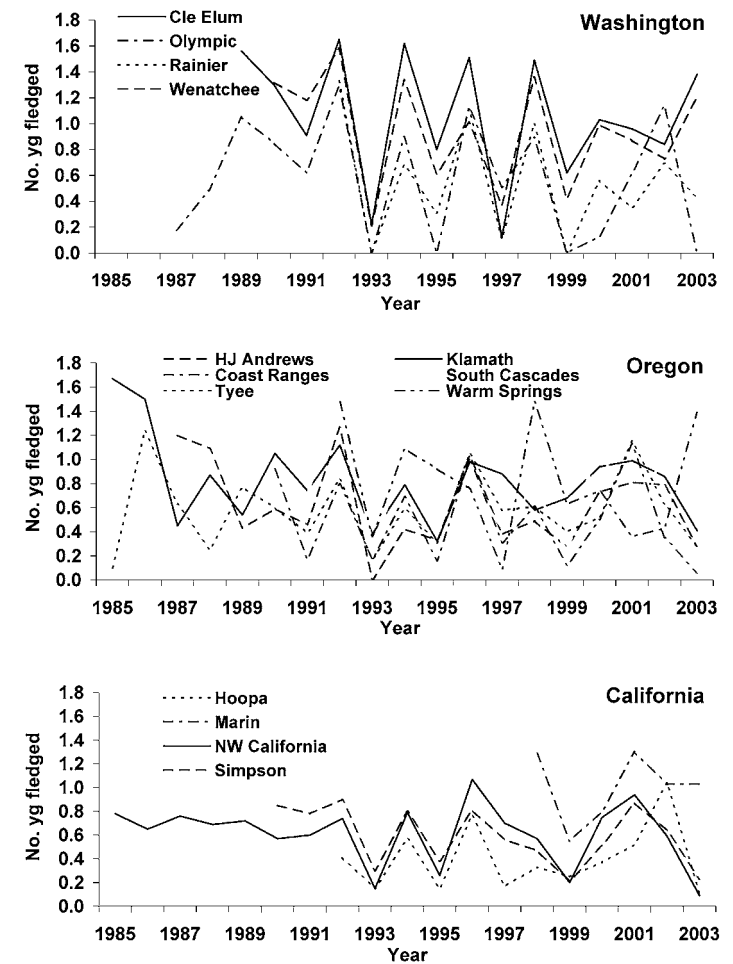
Appendix D. Estimates of annual recapture probabilities ($\hat{p}$) of banded northern spotted owls in 14 demographic study areas in Washington, Oregon, and California. Estimates are from the best AIC_c model for each study area. Study areas that had a sex effect on p include separate columns for males and females.[a]

Year	WEN $\hat{p}$	WEN SE	CLE♂♂ $\hat{p}$	CLE♂♂ SE	CLE♀♀ $\hat{p}$	CLE♀♀ SE	RAI $\hat{p}$	RAI SE
1990			0.899	0.017	0.844	0.021		
1991	0.625	0.050	0.886	0.017	0.826	0.021		
1992	0.643	0.042	0.909	0.019	0.859	0.025		
1993	0.660	0.034	0.860	0.027	0.790	0.034		
1994	0.676	0.028	0.908	0.019	0.858	0.025	1.000	0.000
1995	0.693	0.023	0.882	0.018	0.821	0.022	0.895	0.056
1996	0.708	0.020	0.905	0.018	0.853	0.024	0.890	0.051
1997	0.724	0.020	0.856	0.029	0.785	0.038	0.652	0.083
1998	0.738	0.021	0.904	0.018	0.852	0.023	0.883	0.053
1999	0.753	0.025	0.876	0.020	0.812	0.024	0.560	0.076
2000	0.766	0.029	0.890	0.017	0.832	0.020	0.635	0.078
2001	0.780	0.032	0.888	0.017	0.829	0.020	0.733	0.079
2002	0.792	0.036	0.884	0.017	0.823	0.021	0.789	0.090
2003	0.804	0.040	0.901	0.017	0.848	0.022	0.988	0.189

Year	OLY $\hat{p}$	OLY SE	HJA $\hat{p}$	HJA SE	WSR $\hat{p}$	WSR SE	COA $\hat{p}$	COA SE
1988	0.600	0.163	0.846	0.043				
1989	0.793	0.096	0.829	0.035				
1990	0.818	0.060	0.813	0.029				
1991	0.781	0.055	0.800	0.023			0.863	0.012

	OLY		HJA		WSR		COA	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1992	0.813	0.047	0.790	0.021			0.863	0.012
1993	0.729	0.052	0.784	0.021	0.903	0.033	0.863	0.012
1994	0.764	0.049	0.781	0.022	0.934	0.020	0.863	0.012
1995	0.669	0.056	0.783	0.022	0.892	0.019	0.863	0.012
1996	0.784	0.048	0.788	0.022	0.865	0.019	0.863	0.012
1997	0.749	0.048	0.797	0.020	0.795	0.042	0.863	0.012
1998	0.774	0.049	0.809	0.019	0.906	0.027	0.863	0.012
1999	0.296	0.053	0.825	0.018	0.772	0.033	0.863	0.012
2000	0.746	0.058	0.842	0.019	0.786	0.032	0.863	0.012
2001	0.763	0.055	0.860	0.023	0.707	0.049	0.863	0.012
2002	0.843	0.056	0.880	0.026	0.745	0.037	0.863	0.012
2003	0.698	0.082	0.899	0.030	0.873	0.034	0.863	0.012

	TYE♂♂		TYE♀♀		KLA		CAS	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1986	0.857	0.031	0.805	0.038	0.669	0.227		
1987	0.867	0.027	0.819	0.033	0.609	0.147		
1988	0.876	0.023	0.831	0.029	0.581	0.102		
1989	0.886	0.020	0.843	0.025	0.731	0.077		
1990	0.894	0.017	0.854	0.022	0.851	0.050		
1991	0.902	0.015	0.864	0.019	0.851	0.043		
1992	0.909	0.013	0.874	0.016	0.791	0.042	0.878	0.040
1993	0.916	0.012	0.883	0.015	0.757	0.046	0.832	0.035
1994	0.923	0.011	0.892	0.013	0.858	0.036	0.788	0.029
1995	0.929	0.010	0.900	0.013	0.772	0.043	0.754	0.027
1996	0.934	0.009	0.908	0.012	0.732	0.046	0.734	0.030
1997	0.939	0.009	0.915	0.012	0.748	0.049	0.730	0.031
1998	0.944	0.009	0.921	0.012	0.859	0.035	0.745	0.030
1999	0.948	0.009	0.927	0.012	0.882	0.033	0.775	0.027
2000	0.952	0.009	0.933	0.012	0.881	0.032	0.816	0.025
2001	0.956	0.009	0.938	0.012	0.950	0.022	0.862	0.027
2002	0.960	0.009	0.943	0.012	0.953	0.021	0.906	0.027
2003	0.963	0.009	0.947	0.012	0.897	0.041	0.942	0.025

	NWC		HUP		SIM ♂♂		SIM ♀♀	
Year	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
1986	0.765	0.041						
1987	0.765	0.041						
1988	0.917	0.009						
1989	0.917	0.009						
1990	0.917	0.009						
1991	0.917	0.009			0.859	0.017	0.819	0.019
1992	0.917	0.009			0.859	0.017	0.819	0.019
1993	0.872	0.020	0.868	0.039	0.859	0.017	0.819	0.019
1994	0.917	0.009	0.861	0.027	0.859	0.017	0.819	0.019
1995	0.872	0.020	0.861	0.024	0.859	0.017	0.819	0.019
1996	0.917	0.009	0.867	0.025	0.859	0.017	0.819	0.019
1997	0.917	0.009	0.879	0.025	0.859	0.017	0.819	0.019
1998	0.917	0.009	0.895	0.022	0.859	0.017	0.819	0.019
1999	0.872	0.020	0.914	0.019	0.859	0.017	0.819	0.019
2000	0.917	0.009	0.933	0.017	0.859	0.017	0.819	0.019
2001	0.917	0.009	0.950	0.017	0.859	0.017	0.819	0.019
2002	0.917	0.009	0.965	0.013	0.859	0.017	0.819	0.019
2003	0.872	0.020	0.977	0.016	0.859	0.017	0.819	0.019

	MAR♂♂		MAR♀♀	
Year	$\hat{p}$	SE	$\hat{p}$	SE
1999	0.996	0.007	0.981	0.027
2000	0.989	0.013	0.956	0.040
2001	0.940	0.059	0.786	0.097
2002	0.976	0.024	0.905	0.048
2003	0.976	0.024	0.905	0.048

[a] Acronyms in column headings indicate study area names, as follows: WEN = Wenatchee, CLE = Cle Elum, RAI = Rainier, OLY = Olympic Peninsula, COA = Oregon Coast Ranges, HJA = H. J. Andrews, WSR = Warm Springs Reservation, TYE = Tyee, KLA = Klamath, CAS = South Cascades, NWC = NW California, HUP = Hoopa Reservation, SIM = Simpson, MAR = Marin.

Appendix E. Model averaged apparent survival rates with 95% confidence intervals for male and female northern spotted owls in 4 study areas in Washington (WEN, CLE, RAI, OLY), 6 study areas in Oregon (COA, HJA, WSR, TYE, KLA, CAS), and 4 study areas in California (NWC, HUP, SIM, MAR).
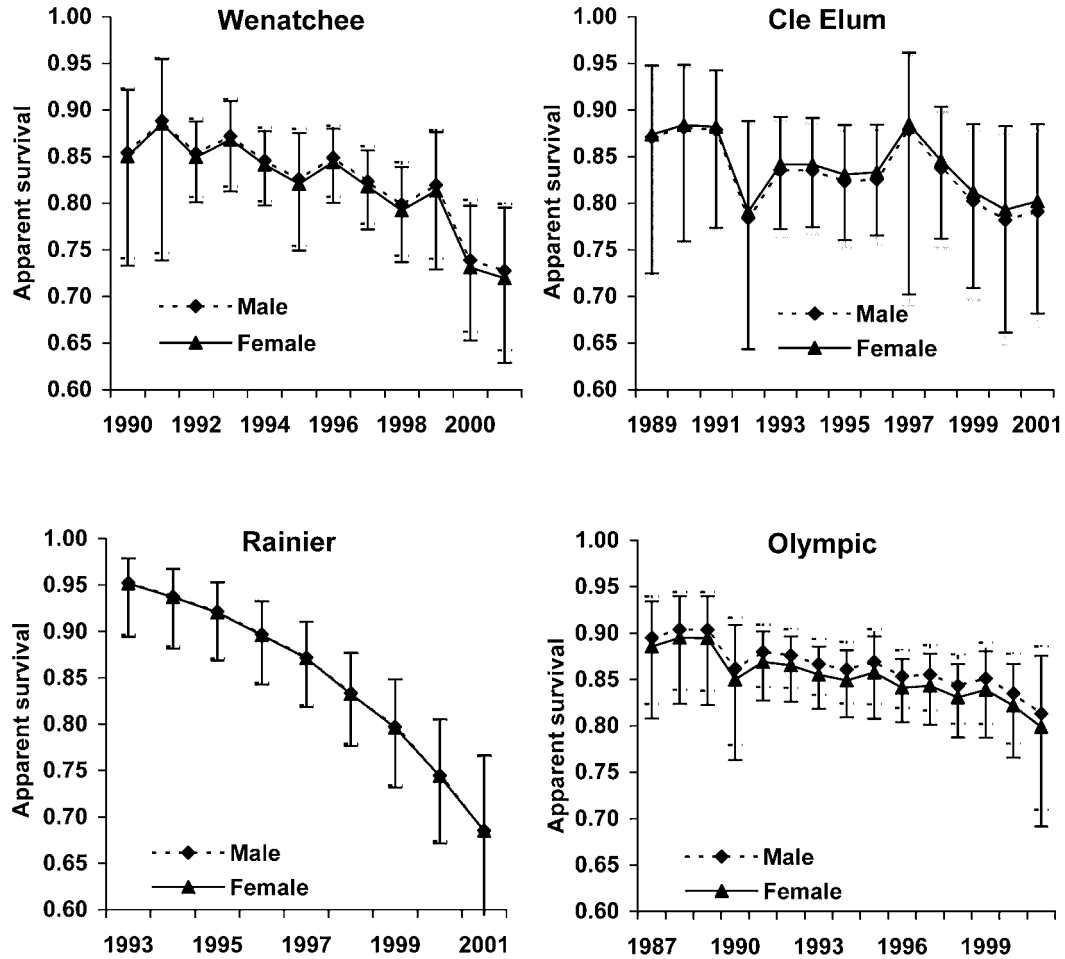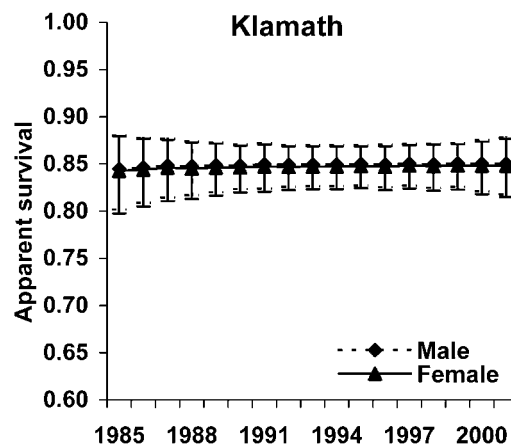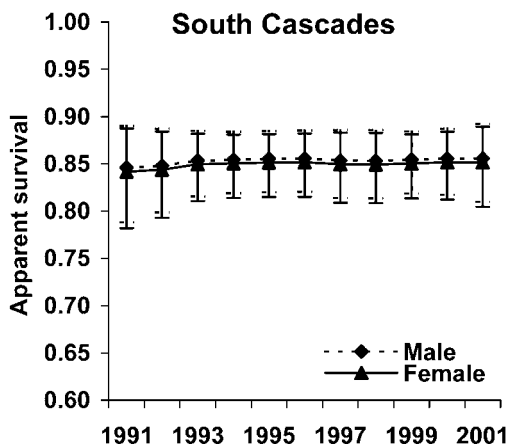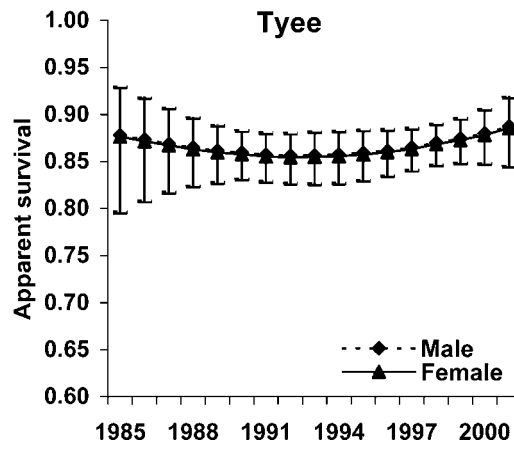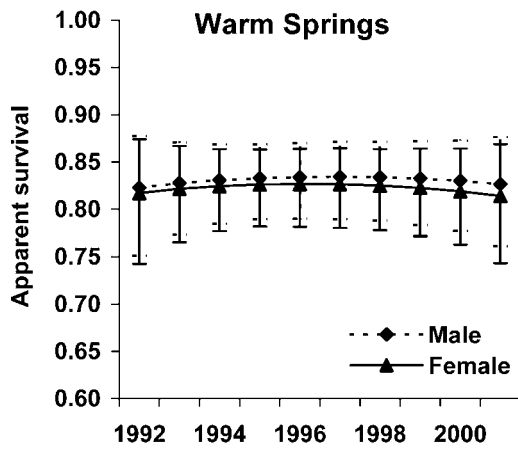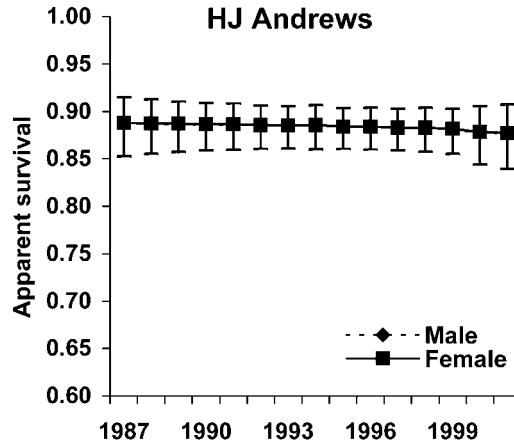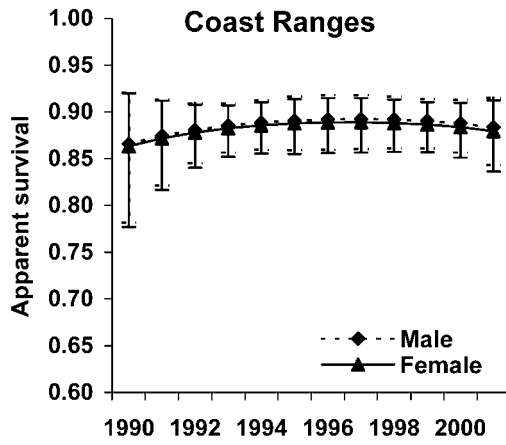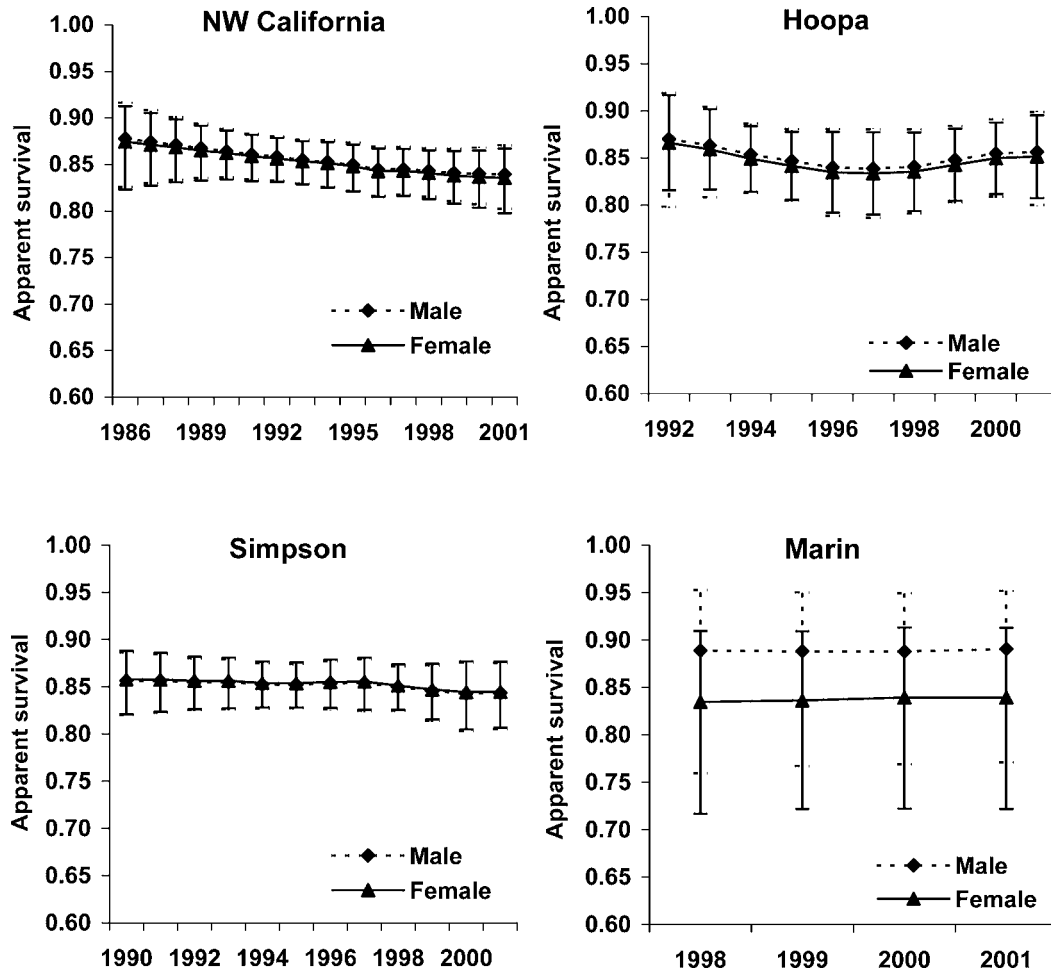
Appendix F. Comparison of Habitat Conditions for Spotted Owls in 14 Demographic Study Areas to Conditions on Federal Lands Surrounding Them

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INTRODUCTION

Several meta-analyses of the demographic rates of northern spotted owls have been conducted over the past 2 decades to estimate fecundity, survival rates, and annual rate of population change for several different study areas. Interpretation of these results and any possible inferences to broader geographic areas have raised some questions about how well the study areas represent the physiographic provinces in which they are located. In fact, Boyce et al. (2005) recently speculated that the study areas likely have better owl habitat and demographic performance than other owl populations. In the latest meta-analysis of the demographic rates of northern spotted owls, Anthony et al. (2004) stated,

> From a statistical standpoint, a formal inference can be made only from the sample of marked and recaptured owls to the population of owls on the study areas in which the marked owls were located. Although the 14 study areas covered a large latitudinal as well as elevational gradient, they were not selected randomly. Consequently, the results of our analyses can not be considered representative, by virtue of the study design, of demographic trends of northern spotted owls throughout their entire range. For example, there were no study areas in the northern Coast Range of Oregon, coastal mountains of southwestern Washington, nor the California Cascades province. However, spotted owl populations in those areas were so low that demographic studies of the type we report here would not be possible. Nevertheless, our 14 study areas were large and covered much of the owl's geographic range, including a variety of land ownerships (private, tribal, mixed private and federal, federal lands) and management strategies. Consequently, we believe that our results are representative of most populations of northern spotted owls on federal lands in the United States.

To evaluate the validity of this statement, we compared habitat conditions in the demographic study areas with conditions on federal lands in the physiographic province outside of the study area boundaries. We asked the question, Is the amount of suitable habitat in the demography study areas similar to that on other federal lands outside of the study areas?

METHODS

The basis for all comparisons was the total area that was capable of growing trees, which we referred to as the "habitat capable area." The percentage of habitat-capable acres in the study areas ranged from 60 to 98% with an average of 84% and a median of 90% (Table F.1). Variation among study areas was a result of variation in topographic conditions and amount of the study areas not capable of providing owl habitat. By using habitat-capable acres as the baseline for comparison of habitat conditions, we eliminated the inconsistency that would have occurred had we evaluated habitat conditions on all lands in the study area boundary. We were not concerned with the percentage of federal ownership in the study areas (Table F.1) because we wanted to compare conditions in the study areas, regardless of ownership, with conditions on federal land outside the study area boundaries to evaluate the statement by Anthony et al. (2004).

We used Program BioMapper (Hirzel et al. 2004) to assign a habitat suitability (HS) score to each pixel of habitat, based on a set of variables that included tree size, elevation, and canopy closure (Davis and Lint 2005). The HS conditions for habitat-capable acres in each demographic study area were then summarized across 5 equal intervals of habitat suitability (0–20, 21–40, etc.) by using owl habitat suitability values from maps created by Davis and Lint (2005). Conditions portrayed by the HS map were those present in 1995–1996 at the beginning of the first decade of implementation of the Northwest Forest Plan (U.S. Department of Agriculture and U.S. Department of Interior 1994). As described in Davis and Lint (2005), HS acres with a

Table F.1. Percent of area classified as "habitat-capable" within 14 spotted owl demography study areas in Washington, Oregon, and California. Asterisks indicate the 8 study areas that are part of the federal monitoring program for the owl (Lint et al. 1999).

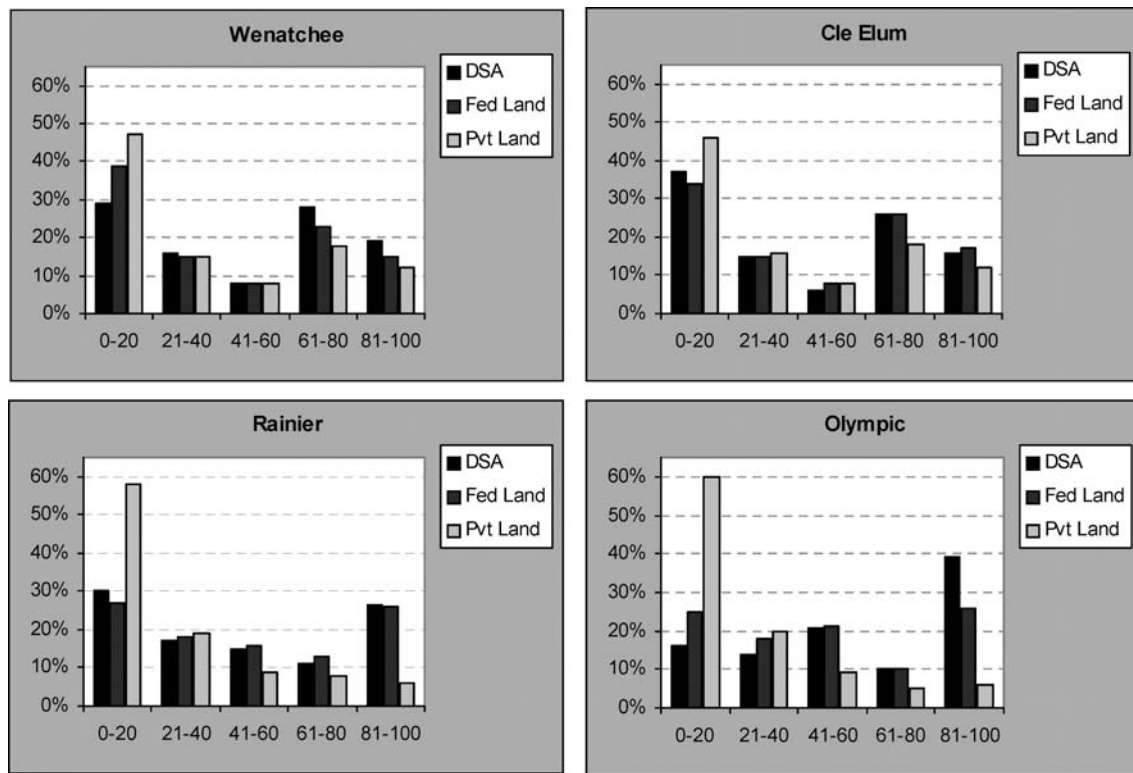| Study area	% of study area classified as "habitat capable"	% of "habitat-capable" area that was federally owned
Washington		
Wenatchee	60	73
Cle Elum*	66	55
Rainier	61	65
Olympic Peninsula*	87	98
Oregon		
Coast Ranges*	98	67
H. J. Andrews*	98	95
Warm Springs Reservation	84	0
Tyee*	94	39
Klamath*	93	47
South Cascades*	83	80
California		
NW California*	93	79
Hoopa Reservation	95	0
Simpson	94	1
Marin	75	43
Mean	84	53

Figure F.1. Histograms for study areas in Washington comparing habitat suitability scores for all lands inside the demographic study areas (DSA), for federal lands (Fed Land) outside the study area in the province, and for nonfederal lands (Pvt Land) in the province.

habitat suitability of 41–100 have characteristics similar to the characteristics of areas where territorial spotted owls have been found. The closer values are to 100, the better the habitat is for owls. Habitat suitabilities of <40 are less similar to the characteristics of owl territories, and values closer to 0 represent poor habitat for the species. We also calculated and summarized the HS values for the habitat-capable acres on federal lands in the remainder of the physiographic province outside of the study areas. In instances where there was more than one study area in a province (e.g., Wenatchee and Cle Elum), the federal portion of the comparison for each study area included the federal land in the other study area.

As an additional measure, values for the 41–60, 61–40, and 81–100 categories of habitat suitability were aggregated into a single category of 41–100 for each demographic study area and the surrounding federal lands because these forests represented conditions most similar to those where owls were known to occur. For each category, we calculated the difference between the percent of habitat-capable lands in the demographic study areas with HS >40 versus that for federal lands surrounding them. We did not account for patch size, landscape arrangement, or management history differences that vary across the landscape and with different landownerships.

RESULTS

The percent of habitat-capable lands varied among each of the demographic study areas and the surrounding federal lands (Table F.1; Figs. F.1–F.3). Comparison of the differences in the percentage of habitat-capable lands in a given category between the lands in the demographic study areas and the surrounding federal lands showed they were within +5% of each other over 80% of the time in 9 of the demography study areas. The remaining 5 study areas had differences from other federal lands ranging from −6 to +16% for 2–3 of the habitat suitability categories. Notable among these were the Marin and Olympic Peninsula study areas, where the combined categories of 61–80 and 81–100 had habitat conditions inside the demographic study areas that were 13–22% higher than the surrounding federal lands. This is because these 2 study areas included large national parks where there has been no harvest of forests. Also in the group of 5 were the Simpson and Hoopa study areas. The Hoopa area was on tribal lands and had a cumulative difference of 15% more habitat-capable acres in the 0–40 category and 15% less in the 61–100 category compared to surrounding federal lands. For the Simpson study area, located on private timber company lands, habitat-capable acres were 14% less in the 0–40 category and 12% more in the 61–100 category than on adjacent federal lands.

Comparisons of HS categories >40, representing suitable owl habitat, revealed that the differences between the demographic study areas and surrounding federal lands were <5% for 9 of the 14 study areas (Table F.2). The differences for the other 5 study areas ranged from 9 to 15%. Three of the latter areas were the Olympic, Hoopa, and Marin study areas, where the differences were expected as noted above. The 2 other study areas were Wenatchee and Simpson where the differences between the lands in the demographic study areas and the surrounding federal lands were +9–14%, respectively.
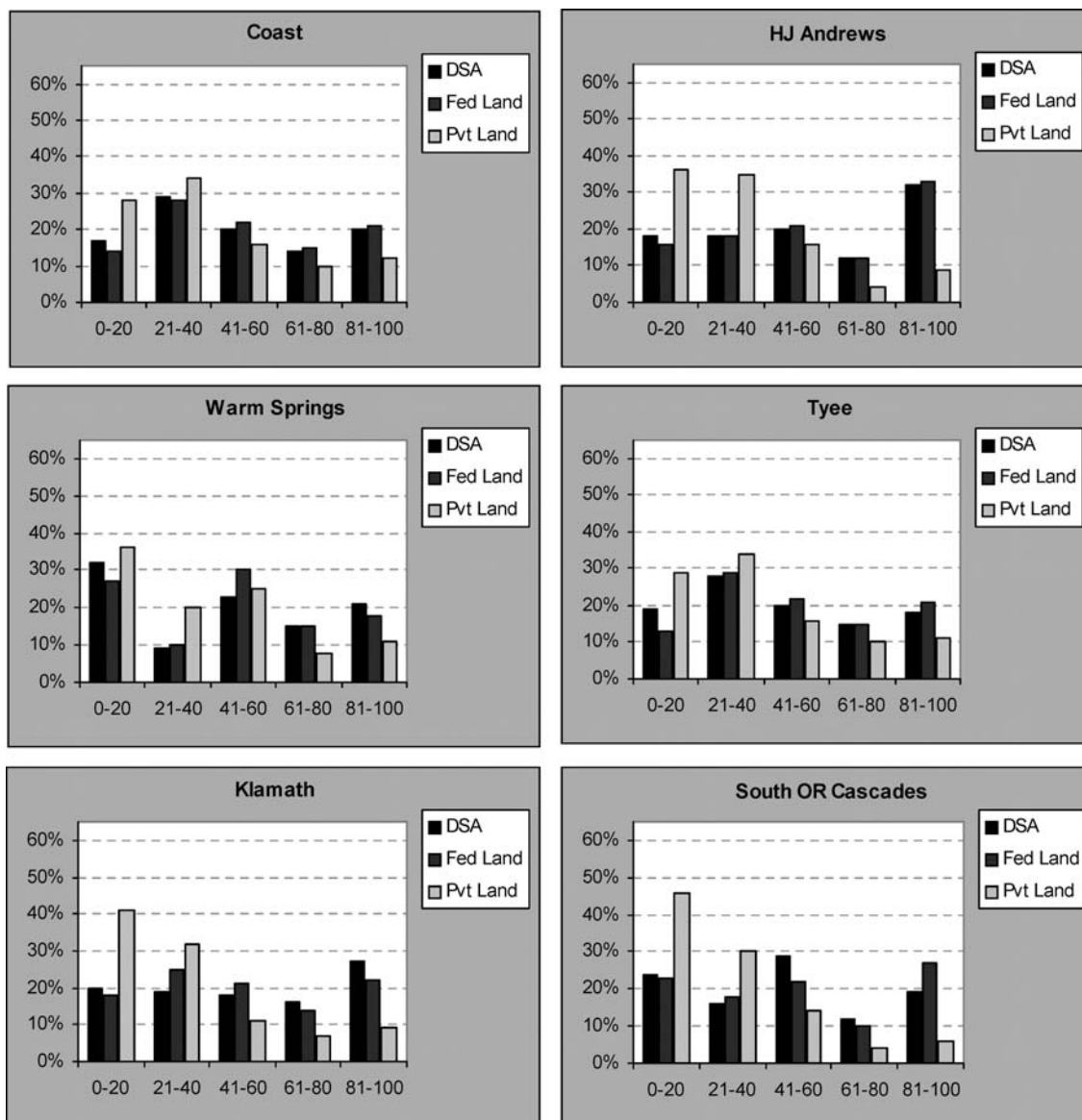
Figure F.2. Histograms for study areas in Oregon comparing habitat suitability scores for all lands inside the demographic study areas (DSA), for federal lands (Fed Land) outside the study area in the province, and for nonfederal lands (Pvt Land) in the province.

DISCUSSION AND CONCLUSIONS

Based on the results of our comparisons, it is evident that the overall habitat conditions for northern spotted owls in the study areas were similar to the conditions on federal lands surrounding the study areas. We expected the Olympic Peninsula and Marin study areas to have higher amounts of suitable owl habitat than the surrounding federal lands in the province because these 2 areas included large national parks where there has been no timber harvest, historically. Even those study areas with little or no federal land have habitat conditions similar to the surrounding federal lands. Our comparisons support the statement by Anthony et al. (2004) that "our 14 study areas were large and covered much of the owl's geographic range, including a variety of landowner-ships (private, tribal, mixed private and federal, federal lands) and management strategies. Consequently, we believe that our results are representative of most populations of northern spotted owls on federal lands in the United States."
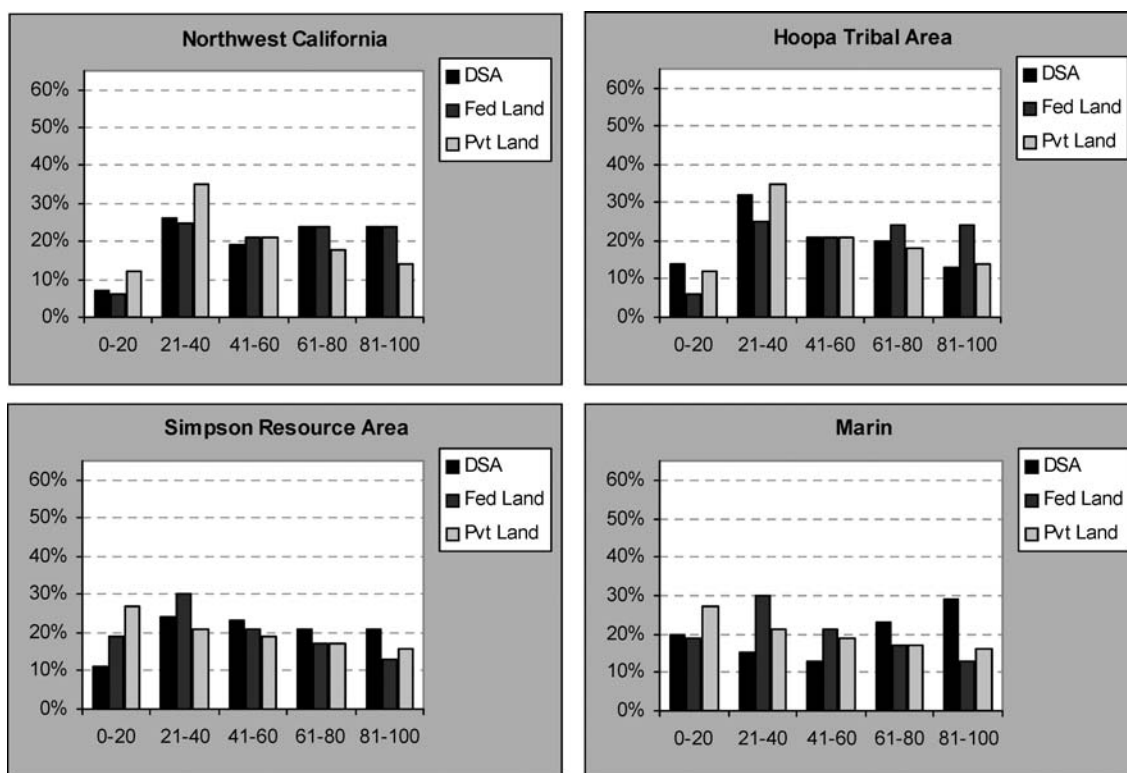
Figure F.3. Histograms for study areas in California comparing habitat suitability scores for all lands inside the demographic study areas (DSA), for federal lands (Fed Land) outside the study area in the province, and for nonfederal lands (Pvt Land) in the province.

Table F.2. Percent cover of lands with habitat suitability scores >40 inside and outside of northern spotted owl demography study areas in Washington, Oregon, and California.[1] Asterisks indicate the 8 study areas that are part of the federal monitoring program for the owl (Lint et al. 1999).

Study area	Geographic province	% HS >40 inside	% HS >40 outside	% difference
Washington				
Wenatchee	East Cascades	55	46	+9
Cle Elum*	East Cascades	48	51	−3
Rainier	West Cascades	52	55	−3
Olympic Peninsula*	Olympic Peninsula	70	57	+13
Oregon				
Oregon Coast Ranges*	Coast Ranges	54	58	−4
H. J. Andrews*	West Cascades	64	66	−2
Warm Springs Reservation	East Cascades	59	63	−4
Tyee*	Coast Ranges	53	58	−5
Klamath*	Klamath	61	57	+4
South Cascades*	West and East Cascades	60	59	+1
California				
NW California*	Klamath	67	69	−2
Hoopa Reservation	Klamath	54	69	−15
Simpson	Coast	65	51	+14
Marin	Coast	65	51	+14

[1] Comparisons included all habitat-capable lands with a habitat suitability category between 41–100. Areas outside each study area included all federal lands within the physiographic province where the study area was located.

A female spotted owl gaurds her young in the "chimney nest" of an ancient Douglas fir tree (photo by Jared Hobbs, http://www.hobbsphotos.com).